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Shoot Growth and Form of Senna Obtusifolia in Response to Soybean and Intraspecific Competition.

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SHOOT GROWTH AND FORM OF *SENNA OBTUSIFOLIA* IN RESPONSE TO SOYBEAN AND INTRASPECIFIC COMPETITION

A Dissertation

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by
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List of Abbreviations

abbreviation	
ai	active ingredient
cos[i]	cosine of angle of incidence between direct solar radiation and a line normal to the leaf surface
DAE	days after emergence
DAS	days after soybean emergence
I	flux density of incident radiation
I_o	flux density of incident radiation measured above the plant canopy
K	coefficient of light interception by the canopy
LAI	leaf area index, m^2 leaf surface per m^2 of ground surface
NI	node index, number of leaf-bearing nodes per m^2 of ground surface
R:FR	the ratio of quantum flux density of red light (655 to 665 nm) to far-red light (725 to 735 nm)

Abstract

Effects of competition on growth and formation of shoot structure in sicklepod (Senna obtusifolia) were examined, with particular emphasis on the effect of nearest neighbors on branching and canopy formation. Sicklepod was established as 1) stands of 26 plants m^{-2} added to soybean, 2) individuals widely enough spaced to produce only interspecific competition when added to soybean, or 3) regularly spaced monoculture stands with 15, 25, 35, and 50 cm interplant distances. Repeated surveys of individual shoots characterized sicklepod growth and shoot structure in terms of position of- and growth at each node.

Sicklepod leaf area, internode elongation, node production, and branching were affected by competition with soybean or other sicklepod, while shoot height was less affected. Branches originating at lower main-stem nodes were the primary means of expanding laterally and forming a closed canopy; these were strongly suppressed by increased competition. Thus, early-season competition with soybean substantially limited the number of leaves in the upper sicklepod canopy that shaded soybean later in the growing season. Decreased rate of branching and more vertical branch growth were detected even before effects of crowding altered shoot height or number of leaves. Branches rapidly filled available area in monocultures ranging over tenfold in stand density; this resulted in ninefold differences in individual shoot dry weight, but no difference in stand dry weight at harvest. Removal of neighboring plants, or planting adjacent to soybean rows, did not alter shoot form. Thus, while sicklepod growth reflected differences in distance to nearest neighbors, it did not respond with directional growth to lateral variation in density of the neighboring canopy. Stand density affected vertical distribution of leaf area before the canopies closed;

but after canopy closure, vertical leaf distribution, leaf area index, and light interception characteristics were not different among stand densities. Models of light interception based on either leaf area index or number of leaf-bearing nodes per unit area were comparable, this suggested that the method of counting nodes provided a simple and rapid method of estimating shading of soybean by sicklepod.

Chapter 1. Introduction

OVERVIEW

Shoot structure of a weed emerging with a crop will partly affect the course of competition. At the same time, shoot structure of an individual is affected by competitive interactions with the surrounding weeds and crop. Plasticity of shoot structure in both crops and weeds can strongly influence the course of competition since the processes of shoot growth and competition affect each other interactively (Maillette 1985, Weiner et al. 1990). Shoot competition for light among weeds and crops is a major source of yield reduction in annual agricultural crops (Radosevich and Holt 1984). Sicklepod (Senna obtusifolia [L.] I. & B.) displays plasticity in shoot structure and variability in its effect on yield of soybean (Glycine max), in particular (Thurlow and Buchanan 1972, Monks and Oliver 1988). Research presented here examines effects of shoot competition on growth and shoot structure in sicklepod.

Shoot structure may be described in terms of number and arrangement of nodes, shoot axes, and leaves; leaf display resulting from these determines potential light interception. Total light interception, and thus growth, depend on both level of incident light as well as light intercepting properties of the shoot. Nearest neighboring plants within a stand can have a significant impact on incident light level. Therefore, the course of shoot competition for light can depend on shoot structure of the individual relative to shoots in the immediate surroundings. Successful placement of leaves at progressively higher positions, relative to neighbors, enables an individual to maintain light interception as the individual and the surrounding canopy grow.

Plants growing in a laterally heterogeneous stand may be exposed to distinctly different levels of available light from different directions. Lateral differences in light availability within a soybean/weed stand may arise: at emergence, due to field preparation; between rows, from planting pattern and cultivation; and above the crop canopy, from relative difference in stature or growth rate. Shoot growth directed toward any additional light available in the canopy will result in increases in light interception and growth.

Both total quantity of light available and the quality of light, as affected by plant canopies, will influence shoot growth (Smith 1982). Altered growth of seedlings, in response to neighbor-mediated changes in light environment, indicates that this interaction may begin early (Ballaré et al. 1987, Novoplansky et al. 1990). Such processes may affect later formation of shoot structure as well, through modifications that preempt impending competition, avoid impending competition, or direct growth toward increased light levels.

Sicklepod often forms a relatively sturdy, tree-like, shoot structure which facilitates characterization of shoot growth and form, and is highly responsive to density and arrangement of surrounding plants. I chose to examine the effects of neighboring plants on the growth and form of sicklepod shoots; specifically aspects of structure that affect vertical and lateral growth as the surrounding canopy forms.

LITERATURE

Sicklepod. Sicklepod is an erect annual dicot species that, although non-native, is a problem weed in some annual crops in the southeastern United States (Teem et al. 1980, Elmore 1986). Shoots, with numerous branches ascending from the base of the main-stem, can grow to over 150 cm in height, yet sicklepod will flower as a single-stemmed plant of less than 10 cm when growth is restricted (Irwin and Barneby 1982). Plasticity in size and form of

sicklepod shoots appears to have a component of genetic control; seed from Guyana and the southern United States, grown in a common garden in the United States, produced different shoot forms, each similar to the population of origin (Irwin and Barneby 1982). The high number of seeds produced by individual plants, together with the persistence of a hard-coated seed in the soil, contribute to the ability of sicklepod to become rapidly established and persist (Retzinger 1984, Bridges and Walker 1985).

Sicklepod will have its greatest effect on crops if it emerges within two to four weeks after the crop (Walker et al. 1984). Sicklepod will usually overtop soybeans in six to ten weeks if it emerges within one to three weeks of soybean planting. This is followed by a rapid increase in sicklepod growth rate (McWhorter and Sciumbato 1988, Monks and Oliver 1988) that eventually places an estimated 70% of the sicklepod leaf area above 90% of the soybean leaf area (Sims and Oliver 1990). The major competitive effect of sicklepod on soybean is, therefore, likely due to late-season sicklepod growth during reproductive growth of soybean. Soybean also significantly affects sicklepod growth; at stand densities of three to five plants m^{-2} sicklepod reduced soybean yield by 30% despite a reduction in sicklepod shoot dry weight by 70% (Sims and Oliver 1990).

The effect of sicklepod on crops is variable. Sicklepod reduced cotton (Gossypium hirsutum) yield by about 35% at 1.1 plants m^{-1} of row (Buchanan and Burns 1971) and reduced soybean yield by about 30% at 3.3 plants m^{-1} of row (Bozsa et al. 1989); yet, the effect of isolated shoots on the adjacent crop was barely detectable in cotton (Byrd and Coble 1991) and soybean (Monks and Oliver 1988). Thurlow and Buchanan (1972) observed that sicklepod had a greater effect on soybean yield when grown 15 or 30 cm from the soybean row than when grown either within or 45 cm from the row. The importance of suppressing early emergent weeds together with the effectiveness of narrow row spacing (Walker et al.

1984, Shaw et al. 1991) suggest that soybean influence on early sicklepod growth is important for control. A key to effective sicklepod management may be in understanding the connection between early season interactions with the crop and late season shoot form, when it is taller than the crop.

Competition, effect of nearest neighbors. Stand-wide measures of weed pressure are often useful in very accurately predicting crop yield losses. However, an individual plant's nearest neighbors will have a greater impact on its growth and ultimate size than will stand-wide factors (Harper 1977, Silander and Pacala 1985). The effect of nearest neighbors on an individual suggests that individual shoots are probably the appropriate level of stand organization at which to examine the interaction of competition with shoot growth and structure. Nearest neighbor effects on an individual plant are most commonly inferred from correlations between individual size and one or more of: 1) distance to neighbors (space available to the individual); 2) neighbor number or size; or 3) a composite function of size and location of specific neighbors.

Some of the first experimental work that examined specific aspects of neighbor influences on individuals focused on the distance to nearest neighbors (Ross and Harper 1972). While "space available" was frequently a significant influence on individual plant growth, the effect of neighbors on the individual is also dependent on factors such as relative time of emergence, evenness of stand arrangement, and identity of neighbor species (Matlack and Harper 1986, Miller and Weiner 1989, Gurevitch et al. 1990). Distance to neighbors becomes a more important predictor of individual growth in relatively even-age stands (Mithen et al. 1984).

The second means of evaluating neighbor effects on an individual involves establishing an appropriate neighborhood size and quantifying individuals within that area.

Number of individuals alone often only accounts for a small part of neighborhood influences on individual growth (Firbank and Watkinson 1987). However, the predictive value improves when neighbors are described in terms of total biomass (Goldberg 1987) or total canopy area (Stoller and Woolley 1985). The third means of describing nearest neighbor effects on an individual are based on models that include number, size, and relative position of neighbors. These models often explain variation in individual size, but become more complicated as additional details are added (Weiner 1982, Silander and Pacala 1985).

These models of neighbor effects on an individual are potentially useful in evaluating crop/weed interactions since specific aspects of the neighborhood such as crop planting pattern can be related to individual growth. An annual crop and the associated weeds are often of essentially the same height and growth form. For this reason, effects of nearest neighbors in a sicklepod/soybean stand are probably adequately described in terms of the area available to the individual (Mithen et al. 1984) which is defined by relative positions of nearest neighbors.

Much of season-long weed control within an annual crop involves exclusion of late-emerging weeds through shading by the closed crop canopy (Radosevich and Holt 1984). Taller canopies of early-emerging sicklepod reduce soybean yield by late-season shading, yet sicklepod emerging four weeks after soybean generally do not reduce soybean yield. This suggests that differing amounts of competition during stand establishment may affect later events that determine yield.

Light in plant canopies. The principal action of light in a plant canopy is as the energy source for photosynthesis, yet it is involved in other processes as well, such as affecting aspects of physiology and morphology through light quantity and quality within the canopy. Light entering a plant canopy will continue unimpeded until it strikes a leaf, or other plant

part, whereupon a portion of the light will be absorbed, and the rest either reflected or transmitted. Light striking a leaf is so attenuated that essentially none is further available for photosynthesis by other leaves at lower canopy levels.

In addition to the quantitative decrease in light flux with depth in the canopy, the spectral qualities of light change within the canopy as well. The most significant effect on light quality is on the phytochrome system and the variety of physiological, morphological and developmental processes controlled by it (Smith 1982). Reflected or transmitted light is depleted of red light and less depleted, or occasionally enriched, in far-red light. This aspect of light quality is usually represented by the ratio of quantum flux in 10 nm wavebands centered at 660 and 730 nm, which is referred to as the ratio of red to far-red light (R:FR).

A variety of models have been formulated to describe light levels within a canopy. These models are broadly categorized as geometrical or statistical (Lemeur and Blad 1974). Geometrical models are based on the shape and locations of individual crowns or foliage elements within the canopy. Statistical models are based on distributions of average leaf properties within the canopy, and are one dimensional and therefore tractable. Their relative accuracy and ease in determining parameters makes them useful for analyses on even height, relatively homogeneous, canopies.

Light entering the canopy consists of both direct solar radiation and diffuse (mostly sky) light, both of which are affected by solar position and sky conditions. Light interception by, or conversely transmittance through, a canopy depends on the distributions of leaf area and leaf orientation as well as the optical properties (absorbance, transmittance, and reflectance) of the leaves (Ross 1981, Myneni et al. 1989). A variety of statistical models estimate light in a canopy based on the various properties of light and canopies.

A relatively simple statistical model, based on Beer's Law, describes the attenuation of direct solar radiation through the canopy (Ross 1981, Monteith and Unsworth 1990). The model estimates the proportion of above-canopy light penetrating directly (without striking a plant surface) to a particular level within the canopy, based on the leaf area and leaf orientation distributions within the canopy. The model is also based on the assumption of random distribution of leaves with respect to the horizontal. It predicts a linear relationship between the logarithm of light level and position in the canopy, expressed as cumulative leaf area from the top. Although theoretically based on direct solar radiation, the model has given very good results when based on average light at a particular level within the canopy (Baldocchi et al. 1985, Zaffaroni and Schneiter 1989).

Shoot structure. Number and relative spatial position of component parts constitute the structure of a shoot. Branching pattern and placement of leaves along shoot axes determine the location of leaves, and ultimately the potential for light interception by the shoot. The form of the individual plant, in turn, affects its ability to compete for light. Relative competitive position of an individual within the canopy can change with growth of the individual as well as that of the surrounding stand of crops and weeds. Components of shoot structure which are subject to change with shoot growth and thus can continuously reshape the individual shoot are: height of shoot relative to neighboring plants; number of branches; vertical and radial distribution of branches; position of leaves along the branches; ability of branches to maintain height in the growing canopy; and secondary reorientation of the leaf lamina (Harper 1977, Fisher 1986).

Plant growth is often indeterminate, even in the relatively short life cycle of many annuals. The resulting plant form can be described as the reiteration of a basic unit of construction (Harper 1977, Waller and Steingraeber 1985). The most common approach to

describing the modular growth of plants is based on White (1979), who described these units as "metamers" which consist of a node, axillary bud, and associated internode section. The individual plant can be viewed as a population of these metamers, the demography of which has been used to describe growth (Maillette 1982) or response of shoot growth to competition (Bazzaz and Harper 1977, Maillette 1985) through birth and death rates of nodes, leaves, or other structures. In an example of weeds in wheat (Triticum aestivum), Maillette (1985) found that higher stand density resulted in fewer leaves due to decreased rate of both leaf formation and leaf death. The same process of counting plant parts was applied to branches and flowers as well. The same approach has also been taken with more complex units, such as branches (Jones 1985, Sprugel et al. 1991). Descriptions of shoot structure, through node demography, usually did not uniquely identify individual nodes, but considered them as a population only. The use of node demography to describe shoot growth can be extended to repeated surveys of the same individuals that identify specific nodes as well as their relative spatial location (Maillette 1986).

Branch formation at nodes not only affects competition through specific placement of leaves relative to height of neighbors, but also increases lateral expansion of the individual. This leads to increased horizontal leaf display, light interception, and thus a higher growth rate. Lateral growth in the absence of competition can rapidly increase light interception, with minimal investment in structural material; as competition increases, increased amounts of shoot structure must be devoted to increases in height (Waller 1986). The value of placing a leaf at a location in a stand is closely related to the light level. Similarly, a branch placed at a particular level within the canopy must grow upward or be replaced, as the surrounding canopy closes, in order to maintain a position favorable for light interception (Lovell and Lovell 1985). Increased shoot size depends on increases in height and width by

an individual; the relative importance of each direction of growth will depend on conditions in the immediately surrounding canopy.

Effects of competition on shoot structure. The most immediate and obvious effect of competition is a reduction in plant biomass. Maillette (1985) and Weiner et al. (1990) have suggested that smaller, more suppressed, individuals in a stand are not just miniature versions of larger individuals; but changes in shoot structure, brought about by competition, can differentially alter their ability to compete for light. The following discussion of typical effects of neighbors on shoot structure focuses on herbaceous dicots since the research is concerned with interference of the annual weed sicklepod in a crop such as soybean.

Uncrowded, larger plants grow rapidly and tend to expand laterally. At the other extreme, the relatively more crowded, or suppressed, plants tend to shift growth upward to maintain at least a part of the shoot in a favorable position for light interception. Shoot heights are usually not very different among individuals in relatively even age stands (Bozsa et al. 1989, Somda and Kays 1990). However, height differences do sometimes develop, with more crowded individuals getting taller early and, occasionally, the less crowded plants becoming taller later in the growing season (Jurik 1991, Weiner et al. 1990).

Competition generally has a greater effect on leaf distribution over the shoot than overall shoot height (Regnier and Stoller 1989, Weiner et al. 1990). Also, leaf area can be larger with less competition from neighbors (Jurik 1991). Increased competition often reduces the amount of leaf area per gram of stem (Jurik 1991, Stützel and Aufhammer 1991) and shifts the leaf area distribution higher on the shoot (Maillette 1985, Weiner et al. 1990).

More intense competition usually decreases number of branches per shoot (Geber 1989, Jurik 1991, Weiner et al. 1990). Branches are often shorter (Geber 1989, Regnier and Stoller 1989) and situated higher on the main-stem of the shoot as competition increases

(Akey et al. 1990, Weiner et al. 1990). Any increase in shoot width, through branching, is often delayed until relatively late in stand establishment, and therefore opportunities for lateral expansion are considerably reduced. The probability of a branch forming at a specific node is affected by competition with neighbors and the presence of other branches on the shoot (Smith 1984, Acock and Acock 1987). Acock and Acock (1987) demonstrated that branch initiation on soybean was very dependent on light level at the node of origin, but only over a limited period of time. Subsequent growth by the branch was apparently under different control than branch initiation.

Growth modifications anticipating or avoiding competition. Seedlings of some herbaceous species alter shoot morphology in response to a R:FR signal reflected from neighboring plants (Franco 1986, Ballaré et al. 1987). Various aspects of shoot physiology and development are affected by R:FR reflected from the surrounding canopy (Kaul and Kasperbauer 1988, Smith et al. 1990). The signal not only has a major role in altering shoot growth but is likely the primary indication of impending competition from nearby plants, especially in a stand of relatively even height (Ballaré et al. 1989). The most rapid change in level of R:FR is near the top of the canopy (Kasperbauer 1987), and the greatest effect of a R:FR signal is usually near the point of incidence along the shoot (Ballaré et al. 1990). The interception of a developmentally active signal at the point of shoot growth strongly suggests that part of the control of shoot growth may be a response to impending competition.

The first suggestions that R:FR plays a role in the interaction between shoot structure and competition are alterations in shoot elongation, leaf area, and tillering induced in seedlings by reflected R:FR (Casal et al. 1986, Ballaré et al 1987). Other evidence suggests that the R:FR signal may have an effect beyond simply indicating relative degree of

crowding. Franco (1986) found that paired seedlings of Kochia scoparia in pots tended to grow away from each other, with the larger individual in the pair showing a lesser degree of directional growth. Novoplansky et al. (1990) found that portulaca (Portulaca oleracea) seedlings, when grown together, produced branches directed away from each other. Light was not limiting in either of these cases, but asymmetry in shoot formation was initiated. Reception of the R:FR signal by the individual shoots clearly had a directional component.

Asymmetrical formation of shoot structure is common in trees growing in a closed canopy. Growth is often reduced on the side of the crown adjacent to another large tree, but increased on a side that is adjacent to a gap in the canopy (Franco 1986). Such alterations in shoot structure serve to improve light interception for the individual through proliferation of sections of the shoot that are intercepting light and reduction in growth of the shaded parts.

Shoot growth that places new leaves in favorable light environments is a key to continued growth. Waller (1986) has suggested that directed and flexible growth that is responsive to light availability will result in a large and successful plant. This may be the process whereby the asymmetry in crown shape develops in many woody species. Sprugel et al. (1991) have suggested that support of continued growth on the shaded side of the crown is wasted energy. Such directed growth in shoot structure may be beneficial in a location that produces abrupt spatial differences in light availability, such as an agricultural field. However, Novoplansky et al. (1989) have shown that pea (Pisum sativum) shoots will support growth in a shaded branch under conditions that otherwise lead to asymmetry in shoot structure. This indicates that support of a branch experiencing competition may be beneficial for certain growth forms in which the shoot, including the temporarily shaded branches, eventually grows taller than the competitor.

RESEARCH

This research deals with the effect of nearest neighbors on sicklepod growth and shoot structure. Effects of neighbors are examined in terms of; 1) how they are reflected in growth and structure of individual shoots and 2) consequences of altered shoot structure for subsequent growth and light interception. Four general issues are addressed, the first concerns particular features of the sicklepod/soybean interaction, while the other three concern the general role of shoot structure in shaping interactions within annual communities:

1. A single sicklepod shoot emerging above the soybean canopy often has very little effect on soybean yield. Does early-season competition with soybean affect later shoot growth and structure, when sicklepod extends above the soybean?
2. Plants increase in size through lateral and vertical growth as the surrounding canopy closes and increases in height. How does distance-to-neighbors affect shoot growth and structure throughout this process?
3. Openings in the stand present a potential for increased light interception. How are sicklepod growth and shoot structure differently affected by the presence of an adjacent opening in the stand?
4. Does distance between plants affect light interception characteristics of closed sicklepod canopies?

The overall objective was to determine response of sicklepod growth and shoot formation to expected conditions in an annual crop with weeds. Planting patterns and other treatment factors were, therefore, selected to simulate competitive situations within the range expected in a soybean crop or sicklepod monoculture. Monocultures produced even-age stand replicates that minimized treatment effects other than distance-to-neighbor. Repeated

node surveys described growth and shoot structure through non-destructive measurements that were sensitive to slight changes in rate and direction of growth.

Effects of adding sicklepod to soybean, either as a stand or individually, on components of sicklepod shoot height and lateral expansion are examined in Chapter 2. Increased level of competition with soybean had the largest relative effect on branch formation, particularly along lower main-stem nodes. Decreased numbers of leaves in the sicklepod shoot above the soybean, by late-season, were a consequence of increased competition which reduced branching during early shoot growth.

Effects of distance to nearest neighbors, with particular emphasis on branches are examined in Chapter 3. Low stand density resulted in increased branching during early shoot growth. This lateral expansion was affected by distance to neighbors before shoot height was affected. Early distance-to-neighbor effects on lateral expansion were expressed before effects on height. A more rapid increase in shoot height followed after the canopy closed. No directional growth was evident in sicklepod shoot structure in response to adjacent openings in the stand. Growth did respond to the increase in average distance to neighbors associated with the creation of an opening in the stand. A consequence of not responding to adjacent canopy openings with asymmetric shoot growth was that all branches continued to grow upward and contribute leaves to the upper part of the shoot.

Light interception characteristics of sicklepod canopies at various stand densities are examined in Chapter 4. Stand density affected individual leaf area and its distribution in an individual shoot before canopy closure, but differences were reduced after the canopy had closed. Light interception characteristics were, then, very similar among stand densities. The method of counting leaf-bearing nodes as a basis for estimating canopy light interception was useful and compatible with node survey techniques of evaluating shoot structure.

Chapter 2. Shoot Structure as Affected by Soybean Interference

INTRODUCTION

Plant shoot form responds to competitive pressure from surrounding plants. Competition can influence shoot biomass, and the number and distribution of leaves (Maillette 1985, Legere and Schreiber 1989, Regnier and Stoller 1989) and branches (Geber 1989, Akey et al. 1990, Weiner et al. 1990). Shoot morphology, principally as it affects light interception, is also one of the factors determining the outcome of competition between neighboring individuals (Fisher 1986, Waller 1986, Legere and Schreiber 1989). This interactions between shoot morphology and competition changes rapidly throughout the growing season of an annual crop with weeds as the canopy closes and increases in height. Models (Barnes et al. 1990, Pike et al. 1990) and experimental measurements (Roush and Radosevich 1985) have suggested that shoot morphology, which reflects previous growth and competitive interactions, may be useful in predicting the relative competitive ability of crops and weeds. The morphological response to competition early in shoot growth may have an effect on all subsequent growth since shoot growth and canopy formation are processes that partly depend on existing shoot structure.

The potential for soybean yield reduction due to competition with sicklepod (Senna obtusifolia [L.] I. & B.) is partly related to sicklepod shoot morphology and changes in growth through the season. Sicklepod shoot morphology is very plastic, responding to both inter- (James et al. 1988, Monks and Oliver 1988, Sims and Oliver 1990) and intraspecific (Bozsa et al. 1989) competition by forming a slender unbranched shoot in a crowded stand, or developing into a profusely branched robust shrub when grown in isolation (personal observation). Despite the fact that sicklepod dry weight was reduced 70% in competition

with soybean (Sims and Oliver 1990), sicklepod in these stands reduced soybean yield by 31% at densities of three to five plants m^{-2} (Banks et al. 1985, Sims and Oliver 1990). Sicklepod will usually overtop the soybean canopy in six to ten weeks when emerging within one to three weeks of soybean planting. A rapid increase in growth rate, following emergence above the soybean canopy (McWhorter and Sciumbato 1988, Monks and Oliver 1988, Sims and Oliver 1990), places as much as 70% of the sicklepod leaf area above 90% of the soybean leaf area (Sims and Oliver 1990). Hence, the major competitive effect of sicklepod on soybean is apparently due to late-season sicklepod growth, during reproductive growth of soybean (Sims and Oliver 1990).

It is currently unclear how early morphological response of sicklepod to competition from soybean affects the potential for later growth of sicklepod when it overtops the soybean canopy. The morphological response of sicklepod to soybean interference was examined in field plots by adding sicklepod to soybean as stands of 26 individuals m^{-2} or as widely spaced individuals. Sicklepod shoot structure was described in terms of the production and location of nodes, leaves, and branches on the main-stem. This permitted nondestructive monitoring of early-season changes in morphology associated with soybean interference and the resulting effect on potential sicklepod growth late in the season.

MATERIALS AND METHODS

Field site and general methods. Experiments were conducted in 1988 and 1990 at the Plant Science Farm, Central Station, Baton Rouge, Louisiana. The soil type at this site was a Mhoon silty clay loam (Typic Fluvaquents, fine-silty, mixed, nonacid, thermic; pH, 6.1; organic matter 2.4%). Soybean crops at this site were incorporated into the soil each year from 1986 through 1990, hence no fertilizers were applied. In 1990, plots were treated with

trifluralin (2,6-dinitro-N,N-dipropyl-4-[trifluoromethyl]benzenamine) at 1 kg ai[1] ha^{-1}, incorporated to a depth of 10 cm prior to planting. All other weeding in both years was done by hand. Centennial soybean was planted June 10, 1988 and May 18, 1990 at a seeding rate of about 30 seeds m^{-1} of row, with north-to-south rows spaced 0.76 m apart. Sicklepod seeds (scarified in concentrated H_2SO_4 for 15 min) were planted by hand at a depth of 1 cm. The initial 3 to 4 seeds per location were thinned to one seedling within one week of emergence.

Rainfall in 1988 totaled only 80 mm during the eight weeks prior to soybean planting (following a 28 mm storm). During the two weeks after planting, only 14 mm of rainfall were received, necessitating irrigation of 8 mm daily for the first 10 days after planting. No irrigation was applied in 1990 since rainfall during the eight weeks prior to planting totaled 174 mm, with 106 mm in the subsequent two weeks.

Plot design was additive, consisting of sicklepod added to soybean in two different planting patterns as detailed below. The pattern designated "sicklepod in stands" was used in both 1988 and 1990 while that designated "widely spaced sicklepod" was used in 1990 only. Sicklepod plants in stands were presumed to experience a balance of inter- and intraspecific competition which was varied as a result of planting sicklepod at two times after soybean planting, and locating sicklepod at different distances from the soybean row. Widely spaced sicklepod was presumed to experience only interspecific competition which varied only with respect to distance from soybean row.

Sicklepod in stands. Sicklepod was added to the soybean in an even rectangular pattern, aligned with the soybean rows. This resulted in three sicklepod rows between each pair of soybean rows. Two sicklepod rows were 13 cm from a soybean row and one row was 38

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[1]Abbreviations: ai, active ingredient; DAS, days after soybean emergence.

cm from, and centered between, two soybean rows. Approximate between-row spacing of 25 cm and within-row spacing of 15 cm produced a sicklepod stand density of 26 individuals m^{-2}. Previous observations on the same site indicated that this stand density would cause little mortality of either sicklepod or soybean (data not shown). Large amounts of stand self-thinning would unpredictably alter the relative size and growth of an individual's neighbors throughout the growing period. Sicklepod was planted either 3 or 10 days after soybean planting. Time from planting to emergence was 3 days less for sicklepod than for soybean so that sicklepod emerged 0 or 7 days after soybean emergence (hereafter designated as 0 DAS or 7 DAS).

The 1988 experiment consisted of 30 plots, 6 replicates each of: soybean without sicklepod; 0-DAS sicklepod with soybean; 0-DAS sicklepod without soybean; 7-DAS sicklepod with soybean; and 7-DAS sicklepod without soybean. In 1990, there were 5 replicates of each treatment, however, the without-soybean treatments were omitted. Treatments were randomly assigned to four-soybean-row by 4 m plots, with the central 2 m of the inner two soybean rows used for sampling (Figure A.4). Six individual sicklepod plants, three from each distance from the soybean row, were sampled from each plot. Individuals were randomly selected from each plot with the provision that there were at least two intervening non-sampled individuals either along or across rows of sicklepod to ensure independence of samples.

Measured components of main-stem structure included: shoot height; individual node heights; and presence, if any, of a leaf or primary (originating from the main stem) branch at that node. In 1988, these nondestructive measurements were made on the same sicklepod plants at 16, 26, 36, and 46 days after sicklepod emergence (hereafter, plant age refers to the time since emergence for that particular species and treatment). Maximum leaf number and

cessation of upward growth occurred about day 90. A final survey of main-stem nodes of sicklepod in stands was made 83 to 85 days after sicklepod emergence in 1988 and 84 to 85 days after sicklepod emergence in 1990 (sequence randomized among plots and treatments for each survey). Informal observation in 1988 suggested that branching and lateral expansion were key responses requiring more detailed description. Hence, 1990 final surveys also included node and leaf heights on primary branches. Shoot dry weights (samples dried at 70 °C for 4 days) for each individual was determined for plants harvested immediately after final node surveys. Season-long survival was determined for all sicklepod within the sampling area of each plot. Soybean measurements at harvest included canopy height and dry weight of two 0.5 m sections of row from each plot.

Widely spaced sicklepod. Another arrangement of sicklepod added to soybean was established in 1990, these produced intraspecific competition only. Three soybean row by 5 m plots, each with a single sicklepod at 0, 5, or 25 cm from the central soybean row. Additional weed-free soybean plots were planted as a check. Sicklepod were planted the same day as the soybean so emergence was generally 3 days before the soybean. Enough widely spaced sicklepod were established for 5 to 7 replicates per sampling.

Surveys of main-stem nodes of widely spaced sicklepod were performed 91 to 93 days after sicklepod emergence, and plants were harvested immediately thereafter. Additional plots of widely spaced sicklepod were harvested at 128 days after sicklepod emergence, when all sicklepod seed were mature, for determination of whole-shoot dry weight and seed yield. Nine 20-cm sections of soybean row (the midpoint of the center section was adjacent to the individual sicklepod) were harvested for dry weight determination as each plot was harvested.

Statistical analysis. Analysis of variance was used to determine the effects of 0- and 7-DAS sicklepod stands on soybean canopy height and dry weight. Since soybean without sicklepod could not be considered a treatment level of the sicklepod stand added to soybean, a second analysis of variance determined the effect of adding the 7-DAS sicklepod stand (the stand expected to have the lesser impact on soybean) to the soybean. Analysis of variance and correlation procedures were carried out for dry weights and components of sicklepod shoot structure (logarithm transformations were applied to dry weights to achieve homogeneity of variances). Data from sicklepod in stands were analyzed for effects of DAS (0 and 7), cm from soybean row (13 and 38), and year (1988 and 1990) as a crossed-nested design with year, DAS, and cm from soybean row as main (fixed) effects and individual plots (random effect) nested within year and DAS. Data from the widely spaced sicklepod were analyzed with cm from soybean as the main (fixed) effect. Since no significant DAS-by-year interactions were found for effects on sicklepod or soybean, data are presented as means of 1988 and 1990. Correlation analyses were performed on residuals from analysis of variance. Resulting coefficients of correlation between shoot dry weight and other measures were compared informally among treatments.

In the Results and Discussion, the direction of a trend among treatment responses is inferred from informal examination of means. Except where stated, such a trend is noted only when analysis of variance identified the overall treatment effect as statistically significant.

RESULTS AND DISCUSSION

Soybean growth. Sicklepod emerging with soybean (0 DAS) reduced soybean height ($P=0.007$) and dry weight ($P=0.019$) relative to soybean grown with sicklepod which

emerged 7 days later (7 DAS; Table 2.1). Soybean dry weight ($P<0.001$) but not height ($P=0.738$) was reduced by sicklepod which emerged 7 DAS, relative to that of weed-free soybean. Soybean adjacent to the widely spaced sicklepod showed no effect of individual sicklepod on the soybean row (Table A.2), similar to previously reported distance-of-influence studies (Monks and Oliver 1988).

Early growth of sicklepod. Time of emergence and distance from the soybean row had little effect on height growth by day 46 (Figure 2.1A; t-tests between treatments with the greatest and least mean heights indicated no significant difference by day 46). Main-stem node number was less for the 7-DAS, 13 cm from soybean treatment (Figure 2.1B). Primary branching displayed the largest and earliest effect among shoot components (Figure 2.1C). Sicklepod located 13 cm from the soybean row at day 36 had fewer primary branches than sicklepod in the other treatments. Also, 7-DAS sicklepod at 13 cm from the soybean row produced fewer branches than those from the 0-DAS treatment. Sicklepod in stands without soybeans reached maximum branch number about day 46 for both DAS treatments (cm from soybean row was not applicable in the uniform stands without soybean rows). Sicklepod in stands with soybean increased little in branch number between days 46 and 84; increases ranged from 1.1 branches (increase from 4.1), for sicklepod emerging 0 DAS and 38 cm from the soybean row to 2.1 (increase from 2.8) for sicklepod emerging 0 DAS and 13 cm from the soybean row. This suggests that treatment differences in late-season branch number result from effects of early-season inter- and intraspecific competition on branch formation along the lower portion of the main-stem.

Sicklepod in all 1988 treatments overtopped the soybean canopy between days 36 and 46 (Figure 2.1A). Reported time intervals for sicklepod height to exceed that of the soybean canopy range from 35 to over 100 days (McWhorter and Sciumbato 1988, Bozsa et al. 1989,

Table 2.1. Height and dry weight of soybean canopy, with and without added sicklepod stands. The soybean were harvested at day 84 (after soybean emergence) in the 0-DAS and without-sicklepod treatments, and day 91 in the 7-DAS sicklepod treatment[a].

Soybean treatment	Height	Dry weight
	cm	g m^{-1} of row
with 0-DAS sicklepod	103 (2.8)	258 (51)
with 7-DAS sicklepod	110 (2.6)	434 (70)
without sicklepod	110 (1.7)	1346 (138)

[a]Notation for treatments: DAS, days after soybean emergence. Values are mean (± mean standard error per year) for 1988 and 1990.

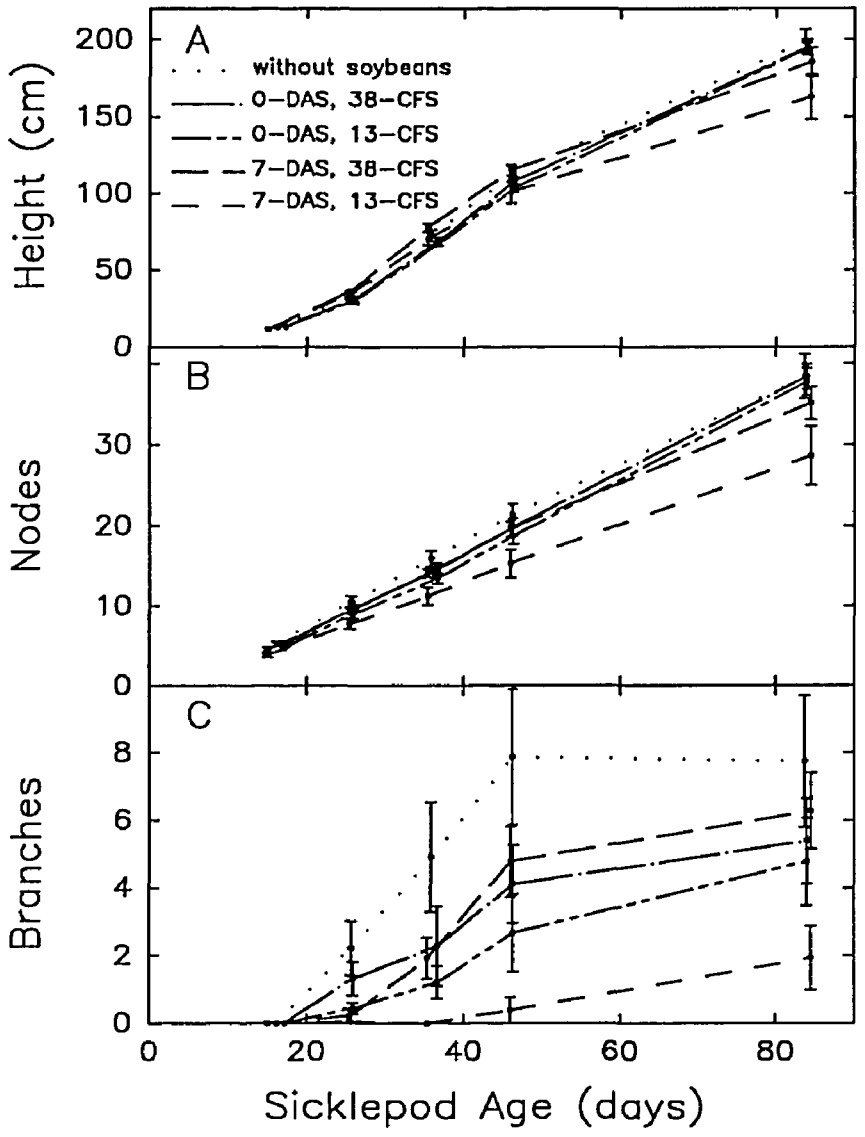

Figure 2.1. Growth of individual sicklepod in stands for 1988; (A) height, (B) number of main-stem nodes, and (C) number of primary branches. Values represent averages over all plots within a treatment and measurement date. Notation for treatments is: CFS, cm from soybean row; DAS, days after soybean emergence. Error bars, which indicate average standard error among individual plants within a plot, are intended to depict plant-to-plant variation within a plot and do not suggest valid statistical comparisons among treatments (some error bars covered ranges too small to resolve on the figure).

Sims and Oliver 1990). This wide range may largely result from yearly variability in sicklepod. Sicklepod monocultures may differ by almost one meter in height from year to year on the same site (Retzinger 1984, personal observation); on this site, the sicklepod in 1988 were taller than in any other year between 1986 and 1990 (data not shown).

Slight effects of soybean interference on height and large effect on branching are consistent with previously observed effects of interference on sicklepod (James et al. 1988, McWhorter and Sciumbato 1988, Bozsa et al. 1989). The height of an individual relative to the surrounding stand can be an important factor determining survival (Lovell and Lovell 1985, Waller 1986). However, season-long survival of sicklepod was uniformly high (most often over 80% in each plot) and was unrelated to treatment in either year (Table A.1).

Sicklepod shoot structure. Decreased distance from the soybean row resulted in shorter individuals with fewer main-stem nodes (Table 2.2), while node 5 (sicklepod developed the first five nodes before the initial survey in 1988) was slightly higher on the plant for sicklepod at 13 cm from the soybean row (sicklepod in stands) and 0 and 5 cm from the soybean row (widely spaced sicklepod). Treatments that increased early-season internode elongation decreased final height. Within a DAS treatment, primary branching and shoot dry weight were at least sixfold more responsive to distance from the soybean row than were shoot height and number of main-stem nodes (Table 2.2). For example, comparison of shoot structural components on 7-DAS individuals at 38 cm from the soybean row, relative to those at 13 cm from the soybean row showed 13 and 22% differences in shoot height and number of main-stem nodes, respectively (Table 2.2), while differences of 194 and 138% were observed in number of primary branches and shoot dry weight. Similarly, for the 0-DAS individuals, shoot height and number of main-stem nodes were essentially equal while primary branches and shoot dry weight differed by 22 and 30%, respectively. Numbers and

Table 2.2. Components of individual sicklepod shoot structure and shoot dry weight measured at day 84 (after sicklepod emergence) for sicklepod in stands and day 92 for widely spaced sicklepod[a].

Treatment		Shoot height	Number of main-stem nodes	Height of node 5[b]	Number of primary branches	Shoot dry weight
		cm		cm		g
1988 and 1990 sicklepod in stands with soybean						
0 DAS	13 CFS	181 (4)	34 (1.7)	30 (2.4)	3.6 (1.0)	27 (5.0)
	38 CFS	185 (5)	35 (1.5)	27 (1.9)	4.4 (1.6)	35 (7.1)
7 DAS	13 CFS	154 (16)	27 (3.7)	34 (2.4)	1.7 (1.0)	16 (4.9)
	38 CFS	174 (10)	33 (2.6)	31 (2.1)	5.0 (1.4)	38 (9.1)
1988 sicklepod in stands without soybean						
		199 (6)	38 (2.1)	28 (2.0)	7.8 (1.5)	47 (8.8)
1990 widely spaced sicklepod						
0 CFS		155 (14)	34 (3.8)	26 (2.1)	11.1 (2.6)	108 (30)
5 CFS		160 (12)	35 (4.1)	26 (1.6)	9.8 (3.4)	107 (47)
25 CFS		165 (5)	40 (1.5)	17 (1.8)	17.6 (1.9)	151 (12)

[a]Notation for treatments: CFS, cm from soybean row; DAS, days after soybean emergence. Values for individual sicklepod in stands are means for 1988 and 1990 (± mean standard error per plot) and for the widely spaced sicklepod are means (±1 standard error). Means of standard errors among individual plants within a plot are intended to depict plant-to-plant variation within a plot and do not suggest valid statistical comparisons among treatments.

[b]Fifth node above the cotyledons.

dry weight of leaves were proportional to individual whole shoot dry weight for all sicklepod (Table A.1).

Mean shoot dry weights of widely spaced sicklepod increased to 189, 309, and 427 g in the 0-, 5-, and 25-cm from soybean row treatments respectively during the interval between days 92 and 128 (compare with values in Table 2.2). This approximate doubling of shoot dry weight was almost entirely due to pod filling. Estimated seed number averaged 3200, 4600, and 6600 individual^{-1} for the 0-, 5-, and 25-cm from soybean row treatments, respectively; numbers consistent with previous observations (Bozsa et al. 1989, Sims and Oliver 1990).

There were no differences in any measure between 0- and 7-DAS sicklepod grown without soybean (1988; combined data shown in Table 2.2), and those plants were similar to sicklepod, with soybean, at 38 cm from the soybean row at either time of emergence in 1988. Apparently, the levels of soybean suppression and intraspecific sicklepod interference are such that the soybean interference does not extend to sicklepod at 38 cm from the soybean row. These are similar to the distance-from-row effects on shoot dry weight seen by James et al. (1988).

Analyses of variance for the sicklepod in stands (Table 2.3) indicated that trends suggested by mean values (Table 2.2) are significant for all responses of shoot components to year and distance from the soybean row. Also, all components of shoot structure except number of primary branches and shoot dry weight responded to DAS. Similar analyses of the widely spaced sicklepod indicated that distance from the soybean row had a significant effect only on the height of node 5. The lack of main effect interactions across data for all structural components (Table 2.3) suggests that DAS and distance from the soybean row are qualitatively similar means of manipulating the relative competitiveness of soybean on

Table 2.3. Significance of treatment effects from analyses of variance for components of sicklepod shoot structure and shoot dry weight at day 84 (after sicklepod emergence) for sicklepod in stands and day 92 for widely spaced sicklepod[a].

Treatment effects	Degrees of freedom	Shoot height	Number of main-stem nodes	Height of node 5[b]	Number of primary branches	Shoot dry weight
Sicklepod in stands						
YEAR	1	*	**	**	*	**
DAS	1	*	**	*		
CFS[c]	1	*	**	**	*	**
YEAR × DAS	1			*		
YEAR × CFS	1					
DAS × CFS	1					
YEAR × DAS × CFS	1					
PLOT(YEAR DAS)	18			*		
CFS × PLOT(YEAR DAS)	18	**	*		**	**
Widely spaced sicklepod						
CFS	2			**		

[a]Notation for effects: DAS, days after soybean emergence; CFS, cm from soybean row. Levels of significance: * $P<0.05$, ** $P<0.01$.

[b]Fifth node above the cotyledons.

[c]Error term for CFS is CFS × PLOT(YEAR DAS).

sicklepod. The significant interaction of year by DAS on height of node 5 (sicklepod in stands) resulted from year-to-year differences in the size of the time-of-emergence effect, but not a qualitative difference between the two years. Additionally, two out of the twenty-two plots of sicklepod in stands contained individuals at 13 cm from the soybean row that were larger than those at 38 cm from the soybean row. This qualitative difference, resulting in a significant interaction between effects of distance from the soybean and plot, suggested that levels of inter- and intraspecific competition vary widely in response to plot-level stochastic factors such as soybean stand establishment. In this regard, height of node 5, a reflection of early-season growth, was the only structural component to display significant plot-to-plot variation, suggesting an early effect of initial conditions within each plot.

Shoot structure/biomass relationships. While distance from the soybean row significantly affected treatment means for shoot dry weight and all components of shoot structure of sicklepod in stands, the range of variation in shoot dry weight and branch number (Table 2.2) suggested a particularly strong association between these two. However, shoot height, number of main-stem nodes, height of node 5 (less consistently), and number of primary branches all displayed similar correlation coefficients with shoot dry weight (Table 2.4) for sicklepod in stands and at 0 and 5 cm from the soybean row in widely spaced sicklepod. This suggests that height and lateral spread were similar in determining productivity of individuals in those cases where inter- or intraspecific shoot competition were presumed to be relatively strong. Branching is frequently reduced by an increase in local crowding in herbaceous stands (Bozsa et al. 1989, Geber 1989, Somda and Kays 1990, Weiner et al. 1990), and often branching is closely related to shoot dry weight (Maillette 1985, Bozsa et al. 1989, Geber 1989). Maillette (1986) and Weiner et al. (1990) have suggested that suppressed annuals had a qualitatively different shoot structure than the more dominant

Table 2.4. Coefficients for correlation between shoot dry weight and components of sicklepod shoot structure. Data from measurements at day 84 (after sicklepod emergence) for sicklepod in stands and day 92 for widely spaced sicklepod[a].

Treatment		Shoot height	Number of main-stem nodes	Height of node 5[b]	Number of primary branches
1988 and 1990 sicklepod in stands with soybean					
0 DAS	13 CFS	0.79**	0.88**	-0.63**	0.72**
	38 CFS	0.52**	0.64**	-0.75**	0.82**
7 DAS	13 CFS	0.92**	0.91**	-0.29	0.62**
	38 CFS	0.91**	0.89**	-0.51**	0.46**
1990 widely spaced sicklepod					
0 CFS		0.99**	0.97**	-0.02	0.94**
5 CFS		0.94**	0.92**	-0.87*	0.99**
25 CFS		-0.36	-0.71	0.43	0.67

[a]Notation for treatments: CFS, cm from soybean row; DAS, days after soybean emergence. Levels of significance for test of correlation coefficient different from zero: * $P<0.05$, ** $P<0.01$.

[b]Fifth node above the cotyledons.

individuals. The change in correlation at 25 cm from the soybean row, for widely spaced sicklepod (bottom of Table 2.4) was consistent with this assertion. However, where competition presumably increased earlier (sicklepod in stands and widely spaced sicklepod at 0 and 5 cm from the soybean row), relationships between shoot dry weight and components of shoot structure were quite similar. This occurred despite an almost sevenfold variation in shoot dry weight among individuals within these treatments. This is consistent with observations by Rice and Bazzaz (1989) that moderate stress affected few indices of allocation.

Height distributions of branches and leaves. By late season, vertical distribution of leaves was quite similar for sicklepod at all distances from the soybean row, both in stands and widely spaced (Figure 2.2, upper portion). Most of the leaves in the sicklepod canopy (data from 1990) were located at heights between 120 and 150 cm, which was above the maximum height of soybean leaves. The major effect of distance from the soybean row was an increase in the total number of leaves on sicklepod plants located 38 (sicklepod in stands) or 25 (widely spaced sicklepod) cm from the soybean row. Within each sicklepod planting pattern, distance from the soybean row only slightly affected branching above the soybean (Figure 2.2, lower portion), but strongly affected branching below the top of the soybean canopy, especially the lower 80 cm of the main-stem. For example, there was a 67% increase in leaves at 25 cm from the soybean row, relative to 0 cm for the widely spaced sicklepod. This was associated with a twofold increase in branches originating below the top of the soybean canopy and no change in those formed above. Hence, decreased competition from soybean increased branching along the lower part of the sicklepod main stem and correspondingly increased leaves in the upper canopy.

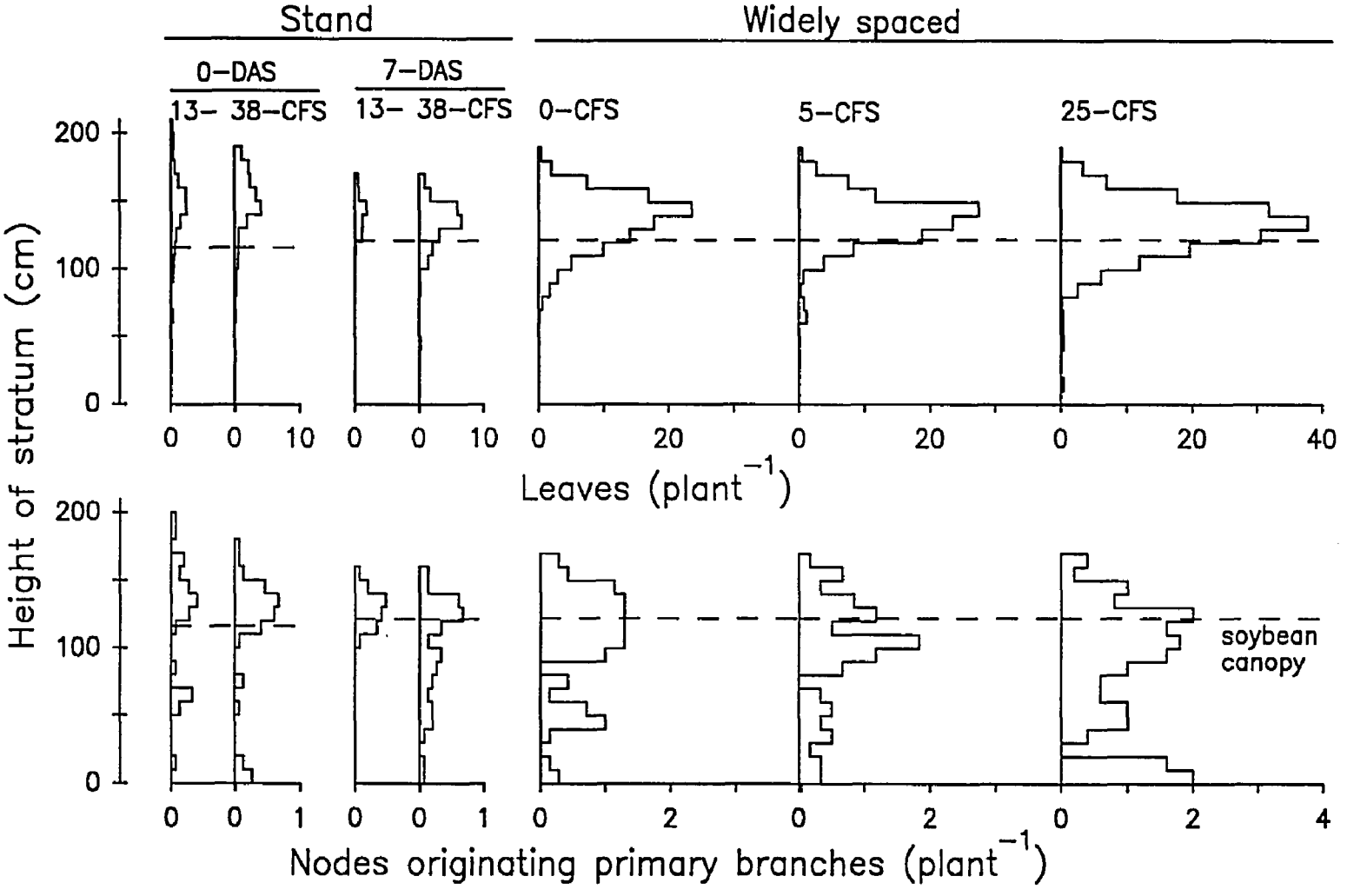

Figure 2.2. Number of sicklepod leaves (upper portion) and nodes originating primary branches (lower portion) within each 10 cm strata. Profiles represent mean values per individual. Dashed line indicates the level of the top of the soybean canopy. Ages are day 84 (after sicklepod emergence) for sicklepod in stands and day 92 for widely spaced sicklepod. Notation for treatments is: CFS, cm from soybean row; DAS, days after soybean emergence.

Sicklepod leaf height distribution did not closely follow that for origin of branches as in some other weeds where both the location and frequency of branches can affect the number and placement of leaves in the canopy (Lovell and Lovell 1985, Fisher 1986, Waller 1986, Regnier and Stoller 1989). Among weed species that overtop soybeans, sicklepod was unlike cocklebur (Xanthium strumarium), which places a significant portion of its leaves within the soybean canopy, but was similar to jimsonweed (Datura stramonium) and velvetleaf (Abutilon theophrasti) in that it eventually locates leaves almost entirely above the soybeans (Regnier and Stoller 1989, Akey et al. 1990). Sicklepod branches originating low in the canopy grew upward at a steep angle and bore leaves at the ends. This added to the total number of leaves in the upper canopy without shifting the distribution vertically. In 1990, the portion of branches originating below the top of the soybean canopy and extending above by late-season was 60 to 80% of the total branches in stands of sicklepod and 80 to 90% in the widely spaced sicklepod.

Decreased branching at lower nodes by individuals located at 13 (sicklepod in stands) or 0 or 5 (widely spaced sicklepod) cm from the soybean row suggests that reduced branching was the major response to early-season influences from immediate neighbors. Dependence of upper canopy development on lower branch formation and the response of both to distance from the soybean row may explain the observation by Thurlow and Buchanan (1972) that sicklepod had the greatest effect on soybean yield when grown at an intermediate distance from the row. Sicklepod may have been located a sufficient distance from the soybean row that branching was not inhibited, yet close enough that the resulting wide sicklepod canopy shaded soybeans deeply later in the season. Early lateral growth is considered imperative for increased productivity during later upward growth (Tomlinson 1982, Lovell and Lovell 1985, Waller 1986). With early-season competition, correlations

indicated possibly similar roles of lateral branching and height growth in determining sicklepod biomass. Results of this study suggest that management tactics that affect early branching of sicklepod would have relatively large effects on soybean yield loss. Such tactics might include narrow row spacing and careful attention to sicklepod emerging in inter-row spaces.

Chapter 3. Nearest Neighbor Effects on Growth and Shoot Form

INTRODUCTION

The morphological plasticity observed in many species is related to the modular nature of plant growth (Lovell and Lovell 1985, Waller 1986). The node, with associated internode segment, leaf, and axillary bud, is a common and convenient modular unit (metamer; White 1979), useful for describing growth. Within species-specific constraints, both biotic and abiotic aspects of the immediate microenvironment can influence the growth at a new node. In turn, growth at a node can strongly affect the interactive processes of shoot growth and shoot competition (Maillette 1985, Weiner et al. 1990). Since shoot growth and form are based on the assembly of node structures, the potential effect of a node on competition depends on the cumulative effect of all previous such interactive processes.

In an annual community, the position of an individual node relative to surrounding canopy is subject to continuous change. Successful competition for light involves a shoot growth pattern that progressively places leaves higher in the canopy (Lovell and Lovell 1985). The increased crowding that often accompanies canopy growth can increase stem elongation (Maillette 1985, Weiner et al. 1990) and number of branches (Geber 1989, Jurik 1991) as well as altering branch placement (Regnier and Stoller 1989, Akey et al. 1990) and leaf position (Maillette 1986, Sims and Oliver 1990). Presumably these typical responses to increased competition tend to maximize light interception of the individual shoot as surroundings change.

Sicklepod (Senna obtusifolia) is a fast growing annual legume species found in disturbed areas, and a problem weed in soybean in the southeastern United States. Higher levels of competition with soybean, through increased proximity to the crop, reduce shoot

dry weight and branching, but generally have little effect on shoot height (James et al. 1988, Chapter 2). Despite a shoot height that exceeds that of the surrounding crop, single sicklepod have little effect in suppressing soybean growth (Monks and Oliver 1988), but sicklepod stands reduce crop yields significantly at densities of 3 to 5 individuals m^{-2} (Banks et al. 1985, McWhorter and Sciumbato 1988, Sims and Oliver 1990).

Branching is the primary means of increased lateral expansion in erect dicots. Plant size of early emerging annuals can largely depend on the amount of lateral expansion established by an individual before the surrounding canopy is effectively closed (Lovell and Lovell 1985, Waller 1986). Any sunlit gap in the canopy adjacent to an individual represents an opportunity for increased light interception through branching if subsequent leaf placement can be maintained above those of competing neighbors. Evidence suggests that morphological response to relative position of neighbors is mediated through light quality effects on the phytochrome system (Smith 1982, Ballaré et al. 1989, Novoplansky et al. 1990). Alterations in growth may delay effects of competition through increased shoot elongation (Ballaré et al. 1987) or branching away from neighbors (Franco 1986, Novoplansky et al. 1990), for example. Control of new growth, such as branches, can be critical since any branch initially requires a diversion of resources from other growing points before becoming a net producer of carbon assimilate. Height relative to nearest neighbors has the most direct bearing on shoot competition (Harper 1977). Therefore, branching must not reduce overall height relative to neighbors.

Apparently the potential for late-season shoot expansion by sicklepod is directly related to early-season effects of neighboring plants on primary branch formation (Chapter 2). We examined the effect of positions of nearest neighbors on the processes of height and lateral growth in individual sicklepod shoots. Growth and shoot form were described by

successive surveys of node number and placement. Specifically, we examined three questions with respect to growth and shoot form: 1) what aspects of node placement and growth determine shoot height and lateral expansion; 2) how are these processes affected by the proximity or spatial arrangement of nearest neighbors; and 3) how do the effects of neighbors at a particular time affect later growth?

MATERIALS AND METHODS

Field site and general methods. Experiments were conducted in 1989 and 1990 at the Plant Science Farm, Central Station, Baton Rouge, Louisiana. The soil type at this site was a Mhoon silty clay loam (Typic Fluvaquents, fine-silty, mixed, nonacid, thermic; pH, 6.1; organic matter 2.4%). Plots were treated with trifluralin (2,6-dinitro-N,N-dipropyl-4-[trifluoromethyl]benzenamine; 1 kg ai[1] ha^{-1}, incorporated to a depth of 10 cm) prior to planting in order to suppress interference from seedling grasses; all other weeding was done by hand. Sicklepod seeds (scarified in concentrated H_2SO_4 for 15 min) were planted by hand at a depth of 1 cm; the initial 3 to 4 seeds per location were thinned to one seedling within one week of emergence. The location of each individual was marked with a small plastic stake as a guide for plot establishment and maintenance. Seedling emergence consistently occurred three days after planting; this produced even-aged sicklepod stands.

Sicklepod was planted on May 31, 1989 and May 22, 1990 in an hexagonal pattern that created radial symmetry with respect to relative position and interplant distance of nearest neighbors. By varying interplant distances with this pattern, four stand densities

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[1]Abbreviations: ai, active ingredient; DAE, days after emergence; LAI, leaf area index, m^2 leaf surface per m^2 of ground surface; R:FR, the ratio of quantum flux density of red light (655 to 665 nm) to far-red light (725 to 735 nm).

were created. Results and discussion related to this stand arrangement will refer to "stand density" data. In 1990, sicklepod was also planted in two patterns intended to simulate spatially asymmetric competitive neighborhoods which would be similar to those encountered in soybean crops. These plots will be referred to as: "gap in stand" where two sicklepod individuals (in the hexagonal arrangement) adjacent to the focal individual were removed (May 21, 1990) and "widely spaced sicklepod" where individuals were located adjacent to soybean rows, (May 18, 1990). Results and discussion will generally focus on data from the stand density plots except where stated otherwise.

Planting patterns and plot layout. Sicklepod planted in an hexagonal pattern was arranged so that each individual had six equidistant nearest neighbors (located at azimuth increments of 60 degrees starting from north; Figure A.6). Interplant distances of 15, 25, 35, and 50 cm produced stand densities of 51.3, 18.5, 9.4, and 4.6 individuals m^{-2} (hereafter referred to as stand densities of 51, 18, 9, and 5 individuals m^{-2}). Each year, four plots (one replicate from each density) were randomly located in each of eight replicate blocks. The size of each plot was partly determined by its planting density; at least five adjacent individuals separated the focus individual from the nearest edge of the rectangular plot (neighbors of nearest neighbors did not have neighbors on the edge of the plot). Each block was 8.4 by 5 m, and the overall area was 19 by 24 m including a 2 m border (9 individuals m^{-2}) around the whole site.

The plots arranged to form a gap in the stand consisted of sicklepod planted in the hexagonal pattern at a stand density of 9 individuals m^{-2}. A gap in the stand was created at planting by not planting the two nearest neighbors situated at azimuths of 60° and 120° or 240° and 300° (Figure A.7). Six plots of each arrangement, west-gaps, east-gaps, and controls were randomly located (with similar border criteria as the density plots) in a 14 by

11 m section planted in the hexagonal array. The plots of widely spaced sicklepod consisted of individual sicklepod planted at one of three distances (0, 5, or 25 cm) from a soybean row and spaced far enough apart to eliminate any effect of intraspecific competition from other sicklepod (see Chapter 2).

Growth and shoot structure. Growth and shoot form were monitored by periodically surveying each node on the central individual in each plot. The surveys established the identity and location of each node, in terms of: 1) axis, main-stem or branch numbered by main-stem node of origin; 2) node number along that axis, counted acropetally; 3) height above the ground; 4) radial distance from the main stem; and 5) azimuth relative to the main stem. Node activity, presence of a leaf or a branch, was noted. Newly produced nodes were included in each survey if the expanding leaf lamina had unfolded at that node. Analyses of shoot structure were, then, based on node position and growth data.

The same focus individuals were repeatedly measured throughout the experiment, with plots being dropped from subsequent measurement and analysis if the individual or any of its immediate neighbors died before the end of the experiment. Plots varying in stand density were surveyed at 19, 36, 39, 54, and 75 days after emergence (DAE) in 1989 and 21, 25, 30, 36, and 77 DAE in 1990. Early-season growth was emphasized in 1990 to characterize the formation of shoot structure during the period before canopy closure. The plots with a gap in the stand were surveyed at 21, 25, 29, 33, and 96 DAE. Individuals in plots of the widely spaced sicklepod were surveyed at 92 DAE. Sicklepod, at these sites, approached maximum height and number of leaves at about 12 to 14 weeks after emergence; this was the time interval chosen for the final measurements of shoot structure and subsequent harvest. At harvest, dry weights were determined after separating leaf tissue from other shoot material and drying at 70 C for 72 hours.

Sample leaf areas from individuals at 36 (border plants in each plot) and 76 DAE (harvested plants) were measured (LI-3100, Li-Cor, Inc.) for the stand density plots and used to estimate individual shoot leaf area. Petiole lengths were also measured at 36 DAE. Estimates of leaf area at each leaf bearing node were made for individuals surveyed at 36 and 76 DAE, based on expected mean areas from multiple regression analysis using stand density, depth in the canopy, and shoot axis of the leaf as independent variables.

Light quality in the canopy. Solar noon ($\pm$1 hour) measurements of laterally transmitted R:FR were made at: 37 through 39 DAE (hereafter referred to as 38 DAE) in 1989; 22, 26, and 31 DAE in the 1990 stand density plots; and 23, 27, and 32 DAE in the gap in stand plots. Measurements were made with a SKR 110 sensor (Skye Instruments Ltd.) which was oriented so that it faced horizontally outward from the plant in one of the four cardinal directions. The 1989 measurements were made with the sensor face adjacent to the main-stem of the individual at 10, 20, and 30 cm depth below the shoot apex. The 1990 measurements were made with the sensor face adjacent to the outside edge of each individual canopy; on the last sampling days in 1990 (stand density and gap) an additional four, similarly positioned, measurements were made on each plant at a level 10 cm below the shoot apex. The east and west facing measurements made in the sicklepod stand with the gap were classified as facing toward the gap or facing away from the gap. Two samples were taken in each cardinal direction, at each level; the quantum flux densities, of each the red and far-red light, were pooled to determine R:FR for that level.

Statistical analysis. The order in which all node survey or light measurements were taken was randomized each time they were made. Analyses of shoot dry weight measures were logarithm-transformed when necessary to achieve homogeneity of variance.

The sicklepod at various stand densities was analyzed using a two factor analysis of variance model, with year and stand density as main effects. Initial analyses included plot as a block factor in a randomized complete block design, but there were consistently no significant block effects or interactions between block and stand density or year. Correlation coefficients between shoot dry weight and components of shoot structure were determined from the residuals of their respective univariate analyses of variance. The effect of stand density on survival of primary branches was determined with a G-test (Sokal and Rohlf 1981). Rao's test (Batschelet 1981) was used to examine randomness in angular distribution of azimuths.

Analysis of whole shoot structure in the plots with a gap in the stand was done in two parts, first a test of the effect of east versus west gaps, and second, a test of gap versus no gap, both used analysis of variance with average weight of neighbors opposite the gap as covariables to account for variability across the area. Branch comparisons used data from branches in 120 degree arcs centered toward the gap and in 120 degree arcs directly away from (180 degrees) the gap. Factors in the analysis of variance models for branches included individual plant and node of origin for the branch as main effects and orientation relative to the gap as nested within individual. Factors in the analysis of variance models for branch weight in the widely spaced sicklepod included distance from soybean row and direction relative to soybean row as main effects.

Factors in the 1989 analysis of variance models for R:FR were stand density and depth as main effects. The 1990 density analysis involved two parts: 1) DAE and stand density effects were analyzed with a repeated measures test in a multivariate analysis of variance model; and 2) at 31 DAE for the stand density (32 DAE for gap) main effects were depth and stand density (or orientation relative to gap).

Stand density effects on shoot structure were analyzed at early- (19 DAE in 1989 and 21 DAE in 1990), mid- (36 DAE), and late-season (75 DAE in 1989 and 77 DAE in 1990); sicklepod ages are hereafter designated 20, 36, or 76 DAE, for all analyses of data from both years. Analyses of variance showed virtually no stand-density-by-year interactions, therefore data are most often presented as two-year means. All significant stand-density-by-year interactions are discussed in the text.

RESULTS

Growth and shoot form. Sicklepod heights were similar among monoculture densities at day 20, diverged so that highest-density monocultures were taller by day 36, then became similar by day 76. Accordingly, stand density affected sicklepod shoot height (Figure 3.1, A and B) at 36 DAE ($P=0.001$), but not at 20 ($P=0.233$) or 76 DAE ($P=0.127$). Shoot height and other measures followed generally similar patterns in 1989 and 1990 (Figure 3.1). Number of main-stem nodes (Figure 3.1, C and D) were similar at 20 DAE ($P=0.334$), but the rate of production was less in the higher stand densities so that differences appeared by 36 DAE ($P<0.001$) and increased through 76 DAE ($P<0.001$). The number of primary branches was significantly different at each period ($P<0.001$ for 20, 36, and 76 DAE), while the total number of leaves (Figure 3.1, G and H) was significantly different at 36 and 76 DAE ($P=0.502$ at 20 DAE; $P<0.001$ at 36 and 76 DAE). The greater net increase in primary branches occurred between 20 and 36 DAE, while the greater net increase in total leaves occurred between 36 and 76 DAE for all stand densities. The rates of increase in numbers of branches and leaves were progressively greater with decreasing stand density in each time interval. Overall number of leaves increased most rapidly late in the season as branches grew and, in the two lowest stand densities, formed secondary branches.

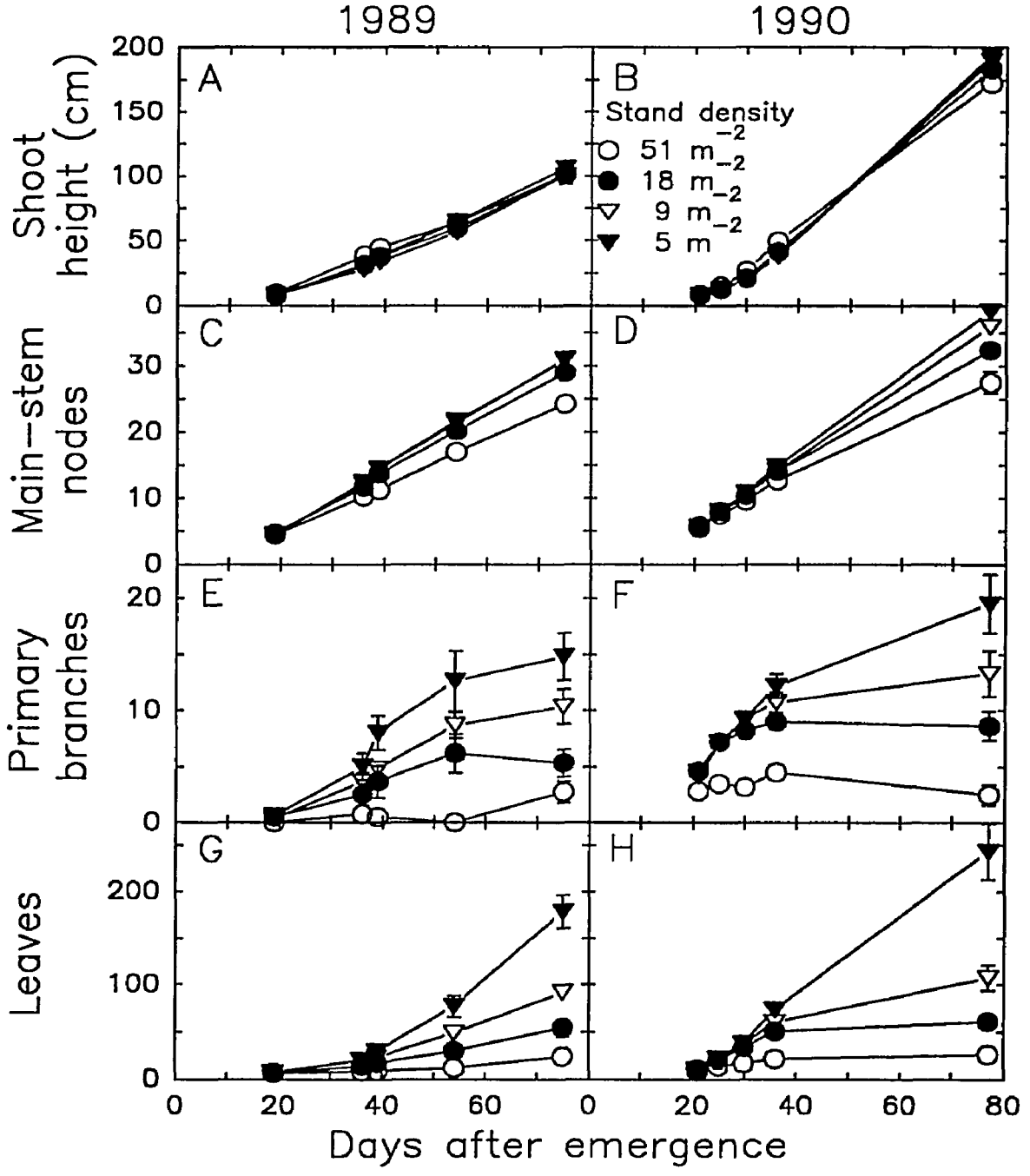

Figure 3.1. Growth of individual sicklepod in each of the four stand densities in 1989 and 1990: (A and B) shoot height, (C and D) number of main stem nodes, (E and F) number of primary branches, and (G and H) number of leaves. Values are means from four to seven (usually six) replicate shoots; error bars are ± 1 standard error.

Increased stand density significantly reduced R:FR ($P<0.001$) along the main-stem at 38 DAE in 1989, but, within each stand density, R:FR was not different at depths of 10, 20, or 30 cm below the main-stem apex ($P=0.823$). Mean R:FR along the main-stem was 0.60, 0.71, 0.76, and 0.82 for the 51, 18, 9, and 5 individual m^{-2} plots respectively. Despite the fact that some open spaces remained between individuals at the three lower stand densities (the canopy closed more slowly in 1989), the influence of the individual shoot canopies were apparently enough to reduce any gradient in R:FR at those depths.

The 1990 measurements were made facing outward at the edge of individual canopies. Stand density had a significant effect on R:FR ($P<0.001$) at the level of the shoot apex (Figure 3.2A); R:FR declined with time ($P<0.001$) over the period 22 to 31 DAE, with no significant interaction of stand density with DAE ($P=0.122$). Measured R:FR at a depth of 10 cm below the shoot apex was reduced relative to that measured at the apex ($P<0.001$) at 31 DAE to: 0.26, 0.48, 0.72, and 0.91 for the 51, 18, 9, and 5 individual m^{-2} plots respectively. The much more rapid decrease in R:FR at the higher stand densities was reflected in the significant interaction of stand density with depth ($P<0.001$).

Shoot structure changed rapidly during the interval between days 20 and 36 in 1990. The number of primary branches per shoot was different among stand densities over this period (Figure 3.1F), the rate of addition of new branches declined between day 20 and day 36. The highest-stand-density shoots were, on average, 29% taller (11 cm; Figure 3.1B) with 14% fewer nodes (2 nodes; Figure 3.1D) than those of the lowest stand density at day 36, but both shoot height and number of main-stem nodes were not different at day 20. The rate of internode elongation at the top of the shoot (Figure 3.2B), although initially somewhat greater in the highest stand density, was not very different among densities and increased throughout the interval. By contrast, the final length (77 DAE) of the same internodes

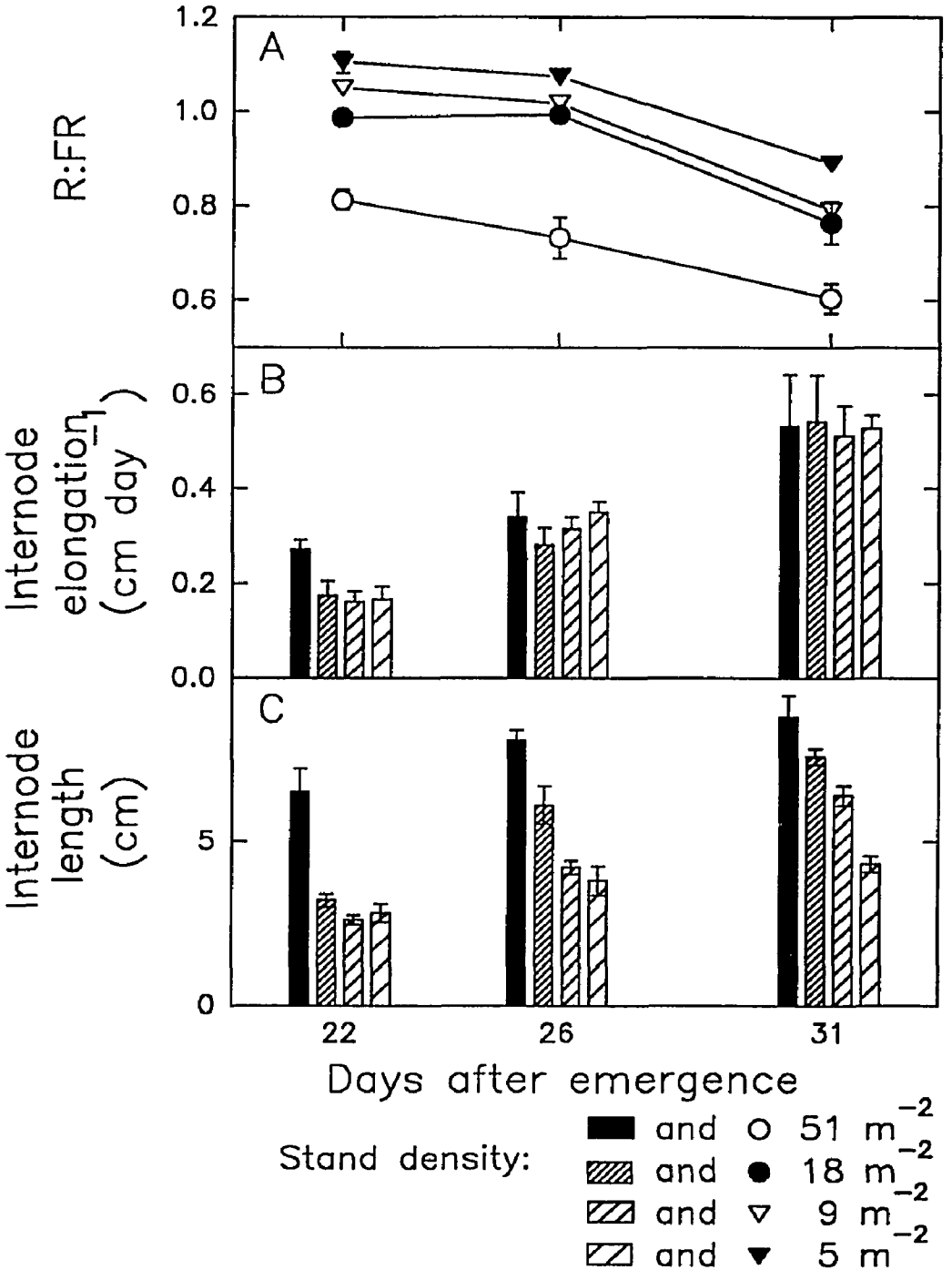

Figure 3.2. Light quality and internode elongation at the sicklepod shoot apex at 22, 26, and 31 days after emergence in each of the four stand densities in 1990: (A) ratio of red to far-red quantum flux (R:FR) transmitted latterally toward the shoot apex, measured at solar noon (±1 hour), (B) the mean rate of internode elongation (cm day^{-1}) for the uppermost two internodes, and (C) the final (77 DAE) mean internode length of the two uppermost internodes. Values are means from five to seven (usually six) replicate shoots; error bars are ±1 standard error.

measured for elongation rate increased with stand density (Figure 3.2C). The first differential effect of the highest stand density on internode elongation occurred between node 2 and node 5, both of which were formed by 20 DAE. At 76 DAE, node 2 heights were 7.0, 6.0, 6.1, and 6.7 cm, while node 5 heights were 21.4, 14.4, 12.7, and 14.6 cm for the 51, 18, 9, and 5 individual m-2 plots respectively. Height at node 2 was based on the first three internode segments (including the hypocotyl), and node 5 included the first six internodes. In the span of three internodes, relative node heights that were not different ($P=0.226$, for node 2) among stand densities became significantly different ($P<0.001$, for node 5).

Differential growth by sicklepod, in response to the tenfold range in stand densities at planting, resulted in a ninefold difference in individual shoot dry weight ($P<0.001$) by 76 DAE (Table 3.1). Stand density had no significant effect on canopy dry weight ($P=0.388$) or leaf area index ($P=0.662$). The 1990 sicklepod canopy produced significantly greater dry weights and leaf area indexes than the 1989 canopy ($P<0.001$ for each, with no interaction of stand density and year) which were 136% and 119% larger, respectively. Two-year means of canopy coverage (leaf overlap of the six radial lines from the focus individual in each plot to its nearest neighbors) were 78, 47, 35, and 24% at 20 DAE and 100, 91, 81, and 74% at 36 DAE for stand densities of 51, 18, 9, and 5 individuals m^{-2}, respectively; all canopies were closed by 76 DAE.

Coefficients of within-stand-density correlation between shoot dry weight and components of shoot structure reflect the strength of these biomass/structure relationships within a stand. Structural components were chosen based on presumed importance in light preemption (shoot height and main-stem nodes), or lateral expansion (number of primary branches and number of leaves). The 76-DAE correlations, between shoot dry weight and

Table 3.1. Individual shoot dry weight, canopy dry weight, and leaf area index at 76 days after emergence[a].

Stand density	Shoot dry weight	Canopy dry weight	Leaf area index
m^{-2}	g	g m^{-2}	
51	17 (3.3)	862 (170)	5.7 (1.28)
18	40 (7.3)	733 (135)	5.2 (0.87)
9	68 (10.0)	640 (95)	4.8 (0.61)
5	158 (16.2)	730 (75)	6.0 (0.83)

[a]Values are mean (± mean standard error per year).

Table 3.2. Coefficients for correlation between shoot dry weight and components of sicklepod shoot structure 76 days after emergence[a].

Stand density	Shoot height	Number of main-stem nodes	Number of primary branches	Number of leaves
m^{-2}	cm			
51	0.86**	0.89**	0.74*	0.86**
18	0.82**	0.79**	0.79**	0.95**
9	0.10	0.33	0.25	0.86**
5	0.80**	0.60	0.35	0.69*

[a]Levels of significance: * $P<0.05$, ** $P<0.01$.

the components of shoot structure were significant at the two highest stand densities only (Table 3.2). Surprisingly, no pattern of significant correlations were found between final, 76-DAE, shoot dry weight and early components of shoot structure at 20 and 36 DAE (Table A.3). Even numbers of primary branches and leaves at 36 DAE were not well correlated with later shoot dry weight within the stand densities.

Stand density effects on branching. The influence of branching on leaf placement in the individual canopies is illustrated in Figure 3.3. Data are from 1989 at 75 DAE and represent the three lowest stand densities only since branching at 51 individuals m^{-2} was relatively rare. Individuals in each column in Figure 3.3 were from within the same block. Most primary branches along the lower one-third of the main-stem were formed by 36 DAE; leaves from these lower primary branches appeared to substantially contribute to the lateral expansion of the shoot at lower stand densities (solid circles, Figure 3.3).

Increased stand density significantly reduced both the number of primary branches formed along the main stem by 36 DAE as well as their survival to 76 DAE (Table 3.3). Stand density also differentially affected the number of branches originating at the top and bottom one-third of the main-stem by 76 DAE (Table 3.4). There was no stand density effect on the number of primary branches on the top one-third segment of the main-stem, but the lower two one-third segments had fewer branches at higher stand densities. The same trend was reflected in the number of branches per main-stem node in each segment. A significant stand-density-by-year interaction ($P=0.032$) in the lower one-third segment was due to the lower rate of branching in 1989 which virtually eliminated lower branches at the higher stand densities.

The number of leaves per branch was reduced at higher stand densities on branches from the lower one-third of the main-stem, but not significantly affected on branches from

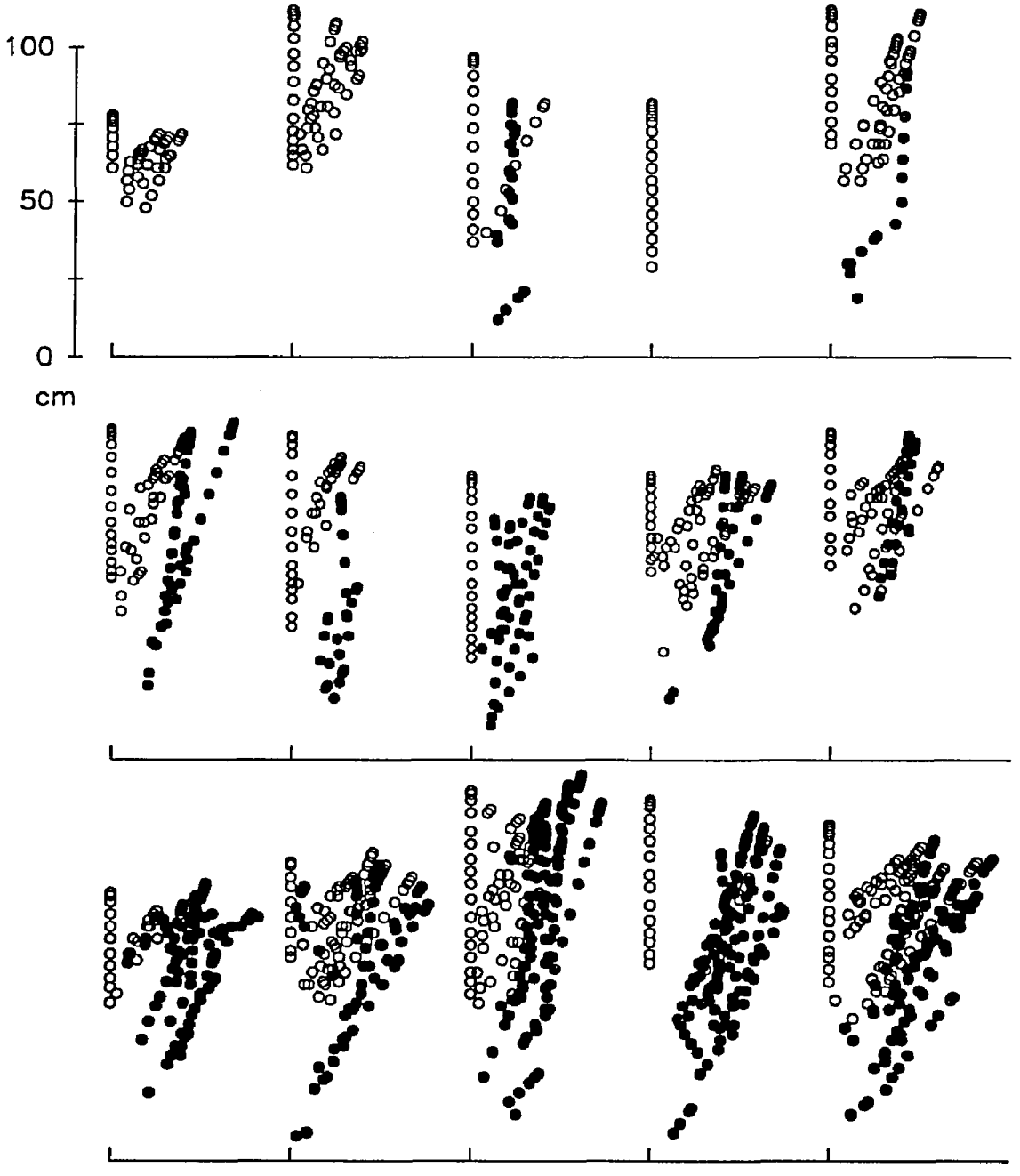

Figure 3.3. Shoot profiles, indicating vertical and lateral position of leaf-bearing nodes relative to the mainstem at 75 DAE in 1990. Five shoots from each of the 18, 9, and 5 individual m^{-2} stands are represented, from the top row to the bottom respectively. Solid circles represent the location of leaves from primary branches originating on the lower one-third-of-shoot-height segment along the main-stem, all other leaves are represented by open circles.

Table 3.3. Number of primary branches initiated per plant by 36 days after emergence and the rate of survival of these branches through 76 days after emergence[a].

Stand density	Branches initiated per plant	Branch survival rate
m^{-2}		
51	3.1	0.125
18	5.4	0.566
9	7.5	0.833
5	9.1	0.880
Analysis:	ANOVA	G-test[b]
Treatment effects		
Density	**	**
Year	**	
Density x Year		

[a]Values are two year means. Levels of significance: * $P<0.05$, ** $P<0.01$.

[b]Test of stand density effect only.

Table 3.4. Primary branch characteristics and levels of significance for stand density. Branches are classified as originating from nodes in one-third of height segments along the main-stem at 76 days after emergence[a].

Stand Density	Number of primary branches	Branches per node	Leaves per branch	Radial distance to apex[b]	Depth of apex in canopy
m^{-2}				cm	cm
Top one-third of main stem					
51	1.5 (0.69)	0.14	4 (0.3)	10 (1.0)	12 (1.2)
18	0.3 (0.17)	0.03	4 (0.6)	11 (2.0)	12 (0.6)
9	1.4 (0.62)	0.12	3 (0.5)	11 (2.1)	22 (2.5)
5	2.1 (0.70)	0.18	4 (0.5)	16 (1.5)	17 (1.5)
Significance:					**
Middle one-third of main stem					
51	0.5 (0.32)	0.07	3 (1.3)	9 (3.1)	33 (7.8)
18	2.2 (0.84)	0.24	7 (0.5)	18 (1.0)	25 (7.6)
9	2.9 (1.02)	0.29	5 (0.4)	19 (1.7)	37 (4.0)
5	4.6 (1.23)	0.50	7 (0.9)	23 (2.4)	41 (4.7)
Significance:	**				*
Bottom one-third of main stem					
51	0.6 (0.15)	0.05	6 (1.6)	--	50 (15.8)
18	4.5 (0.68)	0.33	7 (0.9)	13 (2.0)	59 (10.0)
9	7.3 (0.81)	0.52	10 (0.8)	18 (1.6)	45 (5.7)
5	10.3 (1.16)	0.70	15 (1.7)	27 (1.8)	38 (5.5)
Significance:	**		**	**	

[a]Values are mean (± mean standard error per year). Levels of significance: * $P<0.05$, ** $P<0.01$.

[b]Measured in 1989 only.

the upper two segments (Table 3.4). A substantial portion of the additional leaves on lower branches in the 5- and 9-individual m^{-2} plots were formed on secondary branches, which were never formed on shoots of the two higher stand densities (data not shown). Approximately the same total number of leaves were contributed to the individual canopy by branches from the lower and upper one-third segments on individuals at the highest stand density; while the lowest stand density, eighteen times as many leaves originated on the lower branches as on those from the upper one-third of the main-stem. Branch dry weight followed a pattern, in terms of relative size and significance of stand density, similar to that of leaves per branch.

Primary branches originating along the lower third of the main stem, or at lower stand densities, grew outward so that the branch apex was at a greater radial distance from the main stem (Figure 3.3 and Table 3.4). The effect of stand density was significant for branches on the lower one-third segment only. Depth of branch apex relative to that of the main-stem apex showed no particular trend (Table 3.4); but, while stand density was a significant effect for the upper two segments, it was not for branches on the lower segment. The apparent discrepancy between visual assessments (Figure 3.3), in which lower branch apexes appear to be the same height as main-stem apexes, and means (Table 3.4), in which the branch apex is often 40 to 60 cm below the top of the canopy, is due to the inclusion of all branches in the analyses. Each of the one-third-of-main-stem segments bore branches which varied widely in final length. The branch means (Table 3.4) include smaller branches that are not as prominent on Figure 3.3.

The angle between the main-stem and the first internode of a newly elongating primary branch (prior to elongation of subsequent internodes) was apparently not affected by stand density. The means of all angles measured at all node surveys when the branches had

either one or two nodes were 32, 40, 44, and 50 degrees for the 51, 18, 9, and 5 individual m^{-2} plots respectively; the analysis of variance showed a small level of significance ($P=0.050$). The smaller angle measured at the highest stand density was apparently due to the greater rate of elongation and increased upward curvature (reducing the angle) in early growth of high-density branches (Figure 3.4). Despite the similarity of initial angles, lower branches on higher-stand-density individuals tended to curve upward, decreasing the angle formed with the main-stem; while those on lower-density individuals did not elongate as much and continued mostly-lateral growth before turning upward (Figure 3.4). By 36 DAE, the first internode section of lower branches were significantly longer on shoots in the higher density stands ($P<0.001$).

No shoot, at any stand density (shoots were tested individually), showed significant difference from a random azimuth distribution (i.e. no tendency toward clumping of primary branches in any particular direction) in placement of primary branch apexes at 76 DAE ($P>0.05$ for each). This held true for tests of either all primary branches or those from the lower one-third of the main stem (Figures A.8 and A.9; $P>0.05$ for each). A test of all branch apexes at 76 DAE, which included secondary branches, found a significant ($P<0.05$) tendency toward clumping in two of the eleven shoots from the 5 individual m^{-2} stand density, this due to proximity of a group of secondary branch axes to the branch from which they arose.

Nearest neighbor effects on shoot structure. Mean shoot dry weight of nearest neighbors at 76 DAE (Table A.4) was not a significant covariate affecting height, number of primary branches, or shoot dry weight of the focus individual at 76 DAE ($P>0.05$ for each). The same lack of significant effect, on the focus individual at 76 DAE, was generally true for mean height of the three tallest neighbors at 20, 36, or 76 DAE ($P>0.05$ for each; Table

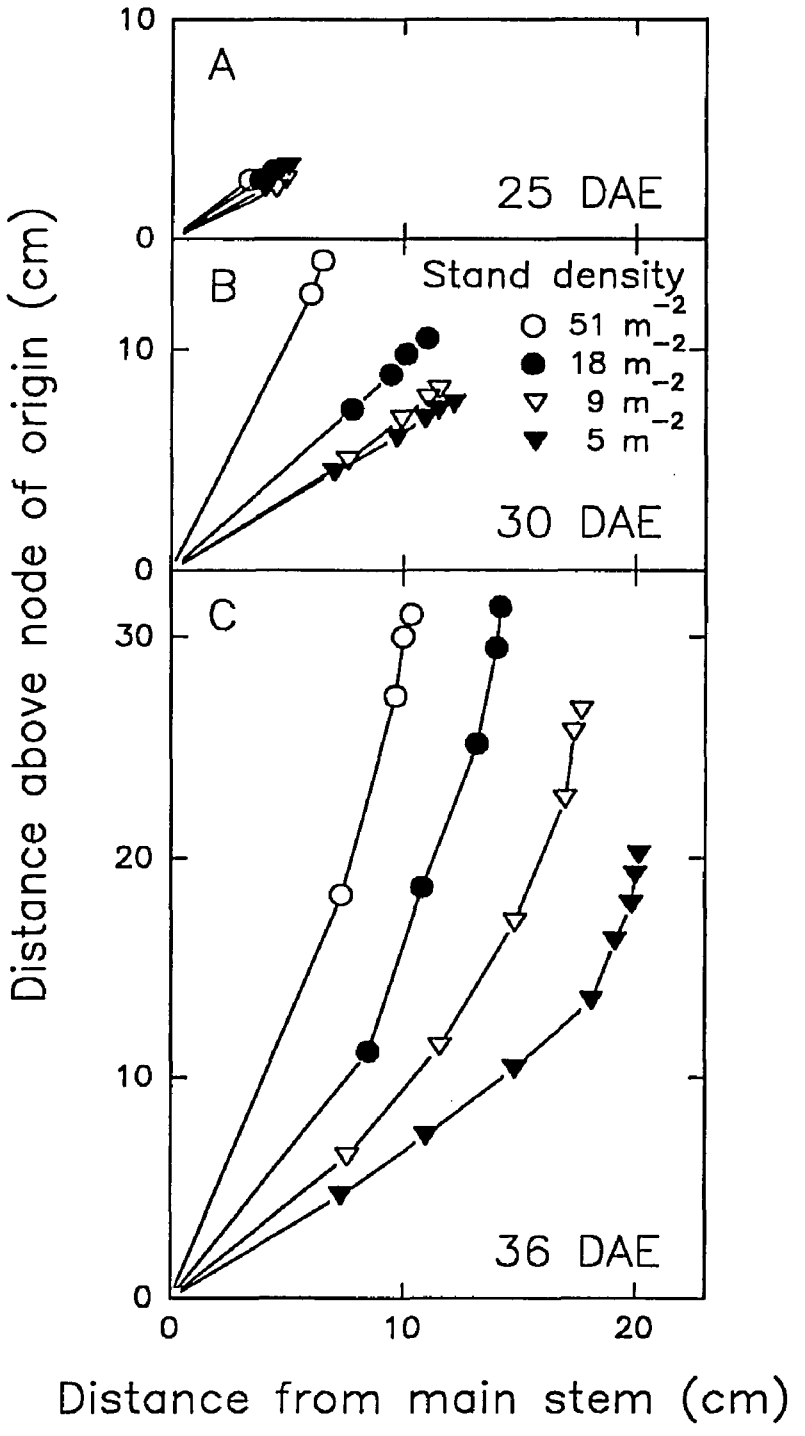

Figure 3.4. Mean vertical and lateral position of nodes on primary branches relative to the main-stem node of origin for the branch at (A) 25, (B) 30, and (C) 36 DAE. Node positions are a composite of those on branches growing from the cotyledon through second node in 1990.

A.4). The only significant effect of neighbor size was height of neighbors at 76 DAE on final height of the individual ($P=0.017$), taller individuals within a given stand density had taller neighbors.

Direction of gap formed in the stand (east versus west) did not significantly affect final shoot dry weight ($P=0.463$), so subsequent analysis involved pooled data from the two treatments. Analysis of variance was used to test the effect of gap on the following: branch length and rate of branch elongation; nodes per branch and rate of increase in nodes per branch; radial distance to branch apex; height of apex; leaves per branch; branch angle with main-stem formed by the first node; and branch angle with main-stem formed by apex. No effect of the gap in the stand was found for any measure of branch size or growth rate ($P>0.05$ for each; e.g. measures of branch size in Table A.6) over the period of 21 to 33 DAE.

Sicklepod adjacent to the gap had a greater shoot dry weight than non-gap sicklepod by 96 DAE (Table 3.5; mean dry weight of similar individuals in the stand density plots in 1990 was 96 g at 76 DAE). At that time, mean branch weight was not different for branches growing into or away from the gap, but there was a significant effect on the number of branches (Table 3.5). The net result was that total branch biomass in the gap was only 10% greater than an equivalent section of branches away from the gap on the same individual. There was clearly an advantage, in terms of biomass, of growing adjacent to the gap; this was distributed among all branches since branches either toward or away from the gap produced more than twice the biomass of an equivalent segment of branches when there was no gap (Table 3.5). The same pattern of overall integration was seen in the widely spaced sicklepod at 5 or 25 cm from the soybean row at 92 DAE; average number of

Table 3.5. Shoot dry weight, branch dry weight, and number of branches at 96 days after emergence of sicklepod with gap in stand. Branch dry weight and number are based on the set of branches from the cotyledon through node seven which grew in a 120 degree arc facing either toward or away from the gap[a].

Treatment effects	Shoot dry weight		Branch dry weight		Number of branches	
	g		g			
no gap	101 (24.7)	*	7.7 (1.73)		2.0 (0.32)	
with gap	150 (22.2)					
toward gap			11.8 (2.02)		3.2 (0.24)	*
away from gap			14.4 (2.62)		2.4 (0.34)	

[a]Values are mean (±1 standard error). Level of significance: * $P<0.05$.

Table 3.6. Ratio of red to far-red quantum flux (R:FR) transmitted laterally toward the shoot apex. Measurements were made at solar noon (±1 hour), with the sensor facing either toward or away from the gap in the stand. Sensor was at the level of the shoot apex on 23, 27, and 32 days after emergence (DAE), and at 10 cm below the shoot apex at 32 DAE[a].

Sensor direction	Height of sensor	23 DAE	27 DAE	32 DAE
toward gap	apex	1.05 (0.010)	1.08 (0.013)	0.91 (0.041)
	-10 cm			0.92 (0.040)
away from gap	apex	1.05 (0.012)	1.02 (0.019)	0.77 (0.053)
	-10 cm			0.72 (0.061)

[a]Values are mean (±1 standard error).

branches and branch dry weight were not significantly affected by growing toward or away from the nearest soybean row (Table A.5; $P>0.05$ for each).

Asymmetry of neighbor location did not affect angular distribution of azimuth for the primary branch apexes. The tests for clumping in the distribution of azimuths found no significant difference ($P>0.05$ for each) from random for each individual either adjacent to the gap in the stand (at 33 DAE; Figure A.10) or in the widely spaced sicklepod (at 92 DAE) plots (data not shown).

At the level of the shoot apex, R:FR declined with time ($P<0.001$) over the period between 23 and 32 DAE (Table 3.6). Although the repeated measures analysis indicated no significant interaction of gap with DAE ($P=0.064$), the reduction in R:FR with DAE was more rapid on the side of the shoot away from the gap. The analysis also showed a significant gap effect, higher R:FR toward the gap, through the same interval ($P<0.015$). At 32 DAE, R:FR was not significantly lower at 10 cm below the main-stem apex ($P=0.659$) and there was no interaction of depth and gap ($P=0.522$).

DISCUSSION

Individuals of the lowest stand density were 9% taller and had 35% more main-stem nodes than those at the highest stand density, yet there were large six-, eight-, and ninefold increases in primary branches, total leaves, and shoot dry weight between sicklepod at the highest- and lowest stand density. This pattern was retained in both years even though early-season branching in 1989 was reduced (Figure 3.1E), probably due to less effective weed control at the beginning of the season (weeds were mostly other sicklepod and seedling grasses). The smaller differences in measures of height compared with primary branches and shoot dry weight were similar to the effect of decreased soybean competition on sicklepod

(James et al. 1988, Bozsa et al. 1989, Chapter 2); consistent with the effect of increased competition on height variability relative to branching and shoot dry weight in many annual canopies (Geber 1989, Somda and Kays 1990, Jurik 1991).

Between-year variation in main-stem height (Figure 3.1, A and B) and the greater height in the high density stand at mid-season (36 DAE) were consistent with observed sicklepod growth at this site in other years. Initially greater shoot height at higher stand density followed by more rapid increase at lower stand density is common in other annuals (Maillette 1985, Jurik 1991); however, Bozsa et al. (1989) found that final height of sicklepod shoots was reduced at extremely low stand densities, where the effects of competition were barely detectable. As with sicklepod in stands added to soybean (Chapter 2), individuals with presumably the greatest level of intraspecific competition (such as those at the highest stand density) produced progressively fewer main-stem nodes through the season thus contributing to the height differential.

Primary branches from the lower-one-third of the main-stem contributed substantially to lateral expansion at the lower stand densities, but also grew strongly upward and maintained active leaves in the upper part of the canopy (Figure 3.3). The basic form of branching and lateral growth in sicklepod involved increased early lateral growth through number (Table 3.4) and shape (Figure 3.4) of lower branches if space was available; as the canopy closed, this was followed by upward growth of many of these branches. Branching on the lower portion of the main-stem apparently increased with decreasing stand density (Figure 3.3, Table 3.4). Primary branches are commonly fewer (Maillette 1985, Somda and Kays 1990, Jurik 1991), smaller (Geber 1989, Weiner et al. 1990), or located higher on the main-stem (Regnier and Stoller 1989, Akey et al. 1990, Weiner et al. 1990) in response to increased crowding in even-aged stands of erect annual dicots. In an analogous situation,

sicklepod reduced the number (Tables 3.3 and 3.4) and size (in terms of leaves, Table 3.4) of lower branches but did not alter position relative to overall canopy height (Figure 3.3, Table 3.4). Hence, addition of lower branches to the canopy resulted in only a twofold difference in density of lower vertical leaf bearing axes despite a tenfold difference in planting densities.

Laterally incident R:FR (Ballaré et al. 1989), from selective transmission and reflection of light in the surrounding canopy, can alter shoot morphology even before the onset of competition for light (Ballaré et al 1987). Developmental response to R:FR appears restricted to the point of interception along the stem (Ballaré et al. 1990). The localized response together with the sharp gradient in R:FR, common near the top of canopies (Kasperbauer 1987, personal observations), indicate that R:FR effects on node formation at the shoot apex may strongly determine the subsequent course of sicklepod shoot development (Kasperbauer 1987, Ballaré et al. 1989).

Differences among stand densities in shoot height and number of primary branches increased between 20 and 36 DAE in 1990 (Figure 3.1 B and F), and are probably affected by R:FR as it interacts with other stand density factors (Casal et al. 1986, Ballaré et al. 1991). Branching is initiated at the top of the shoot, probably before any effects of depth on R:FR; while internode elongation begins similarly at the top of the canopy, it continues at depths greater than 10 cm. Apparently there is little relationship between stand density and the initial rate of internode elongation (Figure 3.2); the increased rate at 31 DAE relative to 22 DAE may be explained solely by difference in individual shoot size (and therefore growth rate) although a direct effect of drop in R:FR over the period cannot be discounted. However, final internode lengths (Figure 3.2C) suggest an effect of R:FR on total duration of elongation. While it is not likely that new internodes elongate at a constant rate,

measured elongation rates and final lengths (Figure 3.2) suggest that the newest internodes at 31 DAE elongated for about 16 days at the highest stand density compared to only 8 days for those at the lowest stand density.

Effects of stand density on some components of shoot structure occurred in a distinct sequence. The first effects of stand density on main-stem growth and structure were on the addition of primary branches. As the plants became larger, differences in shoot height associated with early internode elongation appeared before differences in number of nodes. The greater number of branches per node and nodes per unit shoot height at low stand density resulted in substantially more branches produced when the interplant space was relatively greater; while the greater elongation at higher stand density kept the individual in a position for continued light interception as the canopy increased in height.

Increased stand density (Table 3.4) or competition with soybean (Chapter 2) reduced number of lower primary branches, but did not affect number of upper branches. Reduced branching is a common morphological response to increased competition in sicklepod (McWhorter and Sciumbato 1988, Bozsa et al, 1989) as in many other annual dicots (Maillette 1985, Geber 1989, Weiner et al. 1990, Jurik 1991). Many species place branches higher along the main stem in response to crowding (Regnier and Stoller 1989, Weiner et al. 1990, Akey et al. 1990). When in competition with soybean, velvetleaf and jimsonweed produce almost no branches within the soybean canopy; but produce mostly horizontal branches above the soybean (Regnier and Stoller 1989, Akey et al. 1990). As a weed in soybean, sicklepod generally emerges above the soybean canopy before pod filling stage and may cause significant yield reductions; yet lateral expansion is very limited when lower branches are not produced, since the upper branches contribute relatively few additional leaves to the individual shoot.

Sicklepod monocultures of different planting density formed closed canopies of essentially similar leaf area and dry weight (Table 3.1). It apparently has the capacity to fully close the 50 cm interplant distance of the lowest stand density. The pattern of shoot development suggests this would be less likely with added competition during early shoot growth, even if the competing species was very short-statured. The tendency for a monoculture to form a uniform closed canopy will vary by species and environmental conditions during growth; giant ragweed (Ambrosia trifida) grown at stand densities of approximately 700, 50, and 10 individuals m^{-2} did not converge on a common LAI (Jurik 1991), while sunflower (Helianthus annuus) stands at 6.5, 5.0, and 3.5 individuals m^{-2} all produced a LAI of about 3 (Zaffaroni and Schneiter 1989).

Structure/biomass correlation coefficients within stand density were significant only at the higher stand densities (Table 3.2). This suggests that, while height and lateral expansion are closely associated with shoot dry weight of an individual at high stand density, other factors must increase in importance in determining shoot biomass at lower stand densities. Increased stand density had a similar effect on the pattern in correlation of components of shoot structure with shoot dry weight as did increased soybean competition (Chapter 2). The relatively greater effect of an increase in a unit of branch, or height, at high stand density may lead to increased asymmetric competition between adjacent individuals and thus relatively greater variability in biomass associated with morphology (Weiner and Thomas 1986, Miller and Weiner 1989). With later canopy closure in low-density stands, the period for modifications of shoot structure as the canopy develops is greater, and the duration of intense competition is less. The extended period for potential morphological change would be consistent with the lack of correlation in components of shoot structure at 20 or 36 DAE with final shoot dry weight (Table A.3). Maillette (1985)

also found no correlation between similar components of shoot structure and final biomass until the onset of flowering in Chenopodium album and Spergula arvensis; all correlations were significant for the remainder of the season.

Reduced neighbor influence on one side, either through a gap in the stand (Table 3.5) or increased distance from a soybean row (Chapter 2), resulted in increased total number of branches and shoot dry weight. Although a substantial difference in R:FR was created before canopy closure, no measurable effect was detected in number, rate, or direction of branch growth relative to the gap. Directional differences in level of incident R:FR, without altered total light flux, are associated with early directional difference in branch initiation in Portulaca sativum (Novoplansky et al. 1990), leaf mass in Kochia scoparia (Franco 1986), and length of shoot growth at the top of the crown in Betula pendula (Jones and Harper 1987b). Differences in sicklepod growth and shoot structure associated with asymmetry in the relative position of nearest neighbors were primarily in overall growth, without regard to specific position of nearest neighbors. This was similar to growth and shoot structure in Vicia faba, which was affected by local stand density, not planting pattern (Stützel and Aufhammer 1991).

Differential formation and survival of buds, as well as differential formation and growth of structures at those buds in response to asymmetrical competitive neighborhoods, affect the formation of crown structure in trees (Maillette 1982, Franco 1986, Jones and Harper 1987a). Light effects on these processes, that determine shoot structure, may enhance individual light interception through an asymmetrical crown shape that concentrates growth in favorable parts of the microenvironment. In a forest environment, where height differentials are potentially large and gaps appear infrequently, persistent growth on shaded parts of the crown has limited value (Sprugel et al. 1991). In a fast growing annual canopy,

a relatively more persistent maintenance of growth on shaded branches may ultimately be more beneficial, in terms of eventually placing more leaves at a greater height (Novoplansky et al. 1989). While this growth, and assimilate integration strategy, can lead to larger plants, there are obviously some tradeoffs such as the movement of assimilates to shaded branches, reducing growth on high light branches. However, the apparent separate tendencies of sicklepod to grow laterally outward while maintaining necessary upward growth, suggests that integration of assimilates would probably not reduce sicklepod height relative to the surrounding canopy.

The pattern of node placement by sicklepod suggests that overall R:FR, and not direction of the signal, was the controlling factor. Sicklepod growth was partly in response to some integrated measure of space available such as relative time to canopy closure. Vertical and lateral profiles of shoot structure were both altered in response to neighbors, but radial symmetry with respect to the main-stem was maintained.

Chapter 4. Stand Density Effects on Light Interception

INTRODUCTION

Competition for light is the principal mechanism of weed interference and yield reduction in crops. Morphological characteristics affecting light capture are often better predictors of weed competitive ability than are measures of weed pressure such as stand density or growth rate (Roush and Radosevich 1985, Stoller and Woolley 1985). Extensive shading develops under weed species that emerge above the crop and form laterally spreading canopies. In competition with soybean, jimsonweed and velvetleaf each alter placement of branches so that virtually all are formed above the soybean canopy (Regnier and Stoller 1989, Akey et al. 1990). Sicklepod (Senna obtusifolia), a problem weed in soybean, emerges above the soybean canopy and generally has the greatest effect on yield reduction during the pod filling stage of soybean growth (Sims and Oliver 1990). Individual shoot structure, and thus formation of a canopy above the soybean, is strongly influenced by the level of competition during early shoot development; increased competition reduces the formation of the large lower branches necessary for later canopy expansion (Chapter 2).

In situations where a weed canopy forms above the crop, yield losses will depend directly on the amount of light available to the crop. Light interception by the weed canopy, or conversely, light transmitted through to the crop canopy, is primarily a function of the leaf area and the leaf angle distributions in the canopy (Ross 1981, Monteith and Unsworth 1990). However, soybean yield losses to velvetleaf were better predicted by relatively simple indexes of individual shoot size, such as canopy diameter or projected leaf area, than the sum of individual leaf areas over the entire shoot (Pike et al. 1990). If such easily obtained, reliable, indexes can be obtained nondestructively in conjunction with competition

experiments, they may be useful in characterizing weed canopy light interception over a wide range of competitive situations.

We examine the use of leaf-bearing nodes (node index, NI[1], leaf-bearing node m^{-2}) as a basis for estimating light interception within a sicklepod canopy. Descriptions of shoot growth and morphology based on periodic surveys of all shoot nodes have proven useful in evaluating the interactive processes of shoot competition and the development of shoot form (Bazzaz and Harper 1977, Maillette 1985, Chapter 2). Survey and description of shoot canopy nodes in three-dimensional space determines the number and relative location of all shoot structures. These data were then applied to a model of light interception within that canopy.

Estimates of light levels are commonly based on a model analogous to Beer's Law of light absorption. The model, $I/I_o = \exp(-K \bullet \Sigma \text{ LAI})$, has been used to describe relative light level as a function of leaf area above any point in the canopy (Ross 1981, Monteith and Unsworth 1990). In this model; I/I_o is the proportion of light at a particular position in the canopy (I) relative to that above the canopy (I_o), K is a coefficient of light interception, and Σ LAI is the sum of the leaf area index (LAI, m^2 leaf surface per m^2 of ground surface) above that point in the canopy. The coefficient K is the slope of the linear relationship described by the logarithm of I/I_o as a function of Σ LAI. Beer's Law may be rigorously

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[1]Abbreviations: ai, active ingredient; cos[i], cosine of angle of incidence, between direct solar radiation and a line normal to the leaf surface; DAE, days after emergence; I, flux density of incident radiation; I_o, flux density of incident radiation measured above the plant canopy; K, coefficient of light extinction within the canopy; LAI, leaf area index, m^2 leaf surface per m^2 of ground surface; NI, node index, leaf-bearing nodes m^{-2}; .

applied only to the direct solar beam, however it is often applied to combined direct and diffuse light (Baldocchi et al. 1985, Zaffaroni and Schneiter 1989).

We first obtained sicklepod canopy values of leaf area and leaf orientation which determine LAI and K as they are normally used within the model. The effects of expected normal canopy variation on the range of values for model elements were determined by measuring leaf area and orientation at various stand densities and positions within the canopies. We then examined the possible utility of substituting a cumulative count of leaf-bearing nodes (Σ NI) for that of Σ LAI within the model. If the two differently based coefficients of light interception showed similar fits to the experimental data, we could conclude that one could be reasonably substituted for the other in sicklepod canopies.

MATERIALS AND METHODS

Field site and stand preparation. Sicklepod was planted on May 22, 1990 at the Plant Science Farm, Central Station, Baton Rouge, Louisiana. The soil type at this site was a Mhoon silty clay loam (Typic Fluvaquents, fine-silty, mixed, nonacid, thermic; pH, 6.1; organic matter 2.4%). Plots were treated with trifluralin (2,6-dinitro-N,N-dipropyl-4-[trifluoromethyl]benzenamine; 1 kg ai ha^{-1}, incorporated to a depth of 10 cm) prior to planting in order to suppress interference from seedling grasses; all other weeding was done by hand. Sicklepod seeds (scarified in concentrated H_2SO_4 for 15 min) were planted by hand at a depth of 1 cm; the initial 3 to 4 seeds per location were thinned to one seedling within one week of emergence. The location of each individual was marked with a small plastic stake as a guide for plot establishment and maintenance. Seedling emergence consistently occurred three days after planting; this produced even-aged sicklepod stands.

Sicklepod planted in an hexagonal pattern was arranged so that each individual had six equidistant nearest neighbors (located at azimuth increments of 60 degrees starting from north; Figure A.6). Interplant distances of 15, 25, 35, and 50 cm produced stand densities of 51.3, 18.5, 9.4, and 4.6 individuals m^{-2} (hereafter referred to as stand densities of 51, 18, 9, and 5 individuals m^{-2}). Four plots (one replicate from each density) were randomly located in each of eight replicate blocks. The size of each plot was partly determined by its planting density; at least five adjacent individuals separated the central individual from the nearest edge of the rectangular plot (neighbors of nearest neighbors did not have neighbors on the edge of the plot). Each block was 8.4 by 5 m, and the overall area was 19 by 24 m including a 2 m border (9 individuals m^{-2}) around the whole site. Whole-shoot leaf area and light extinction measurements were analyzed for plots in which the central shoot and those in the immediate vicinity survived through 77 days after emergence (DAE); thus sample size for these data were 6, 5, 7, and 6 for the 51, 18, 9, and 5 individuals m^{-2} stands respectively.

Estimates of LAI were based on surveys of the leaf-bearing nodes from the same sicklepod shoot in each plot at 36 and 77 DAE. Node heights were recorded at each node survey. Multiple regressions, used to produce expected mean leaf areas for each node, were based on leaf samples taken from border plant at 36 DAE and from the surveyed shoots at 77 DAE. In addition to stand density, polynomial regression models for 36 DAE included ordinal node position below the top of the shoot, while those for 77 DAE included depth-in-canopy and type of shoot (main stem, large lower branch, or any other branch) as independent variables. Analyses of stand density effects on individual leaf areas were made with leaf area samples from main-stem nodes 6 through 9 (fully expanded leaves near the top of the canopy) at 36 DAE, as were an analysis of petiole length on the same leaves.

Similarly, individual leaf areas were compared at 77 DAE using leaf samples from the 40 to 100 cm depth within the canopy.

Leaf orientation. Measurements of leaf angle (orientation of leaf lamina) were made in the morning (solar zenith $> 45°$) and at mid-day (solar zenith $< 30°$) over a three day period immediately after the 36 DAE survey. These were relatively cloud free and calm days. Leaves were systematically selected from within the center area of each plot. Leaves were sampled at the top of the canopy where they were exposed to full sunlight and at 30 cm below the top of the canopy. Each of the six leaflets per leaf were measured and counted as independent samples since final lamina-orientation appeared to be mostly dependent on pulvinar movement.

Leaf angles were calculated from measurements of the elevation of the leaf lamina relative to the east and north horizons. From these two unit vectors, a unit vector normal to the leaf surface was obtained and used to determine leaf angle relative to direct solar radiation. Solar time was recorded with these measurements in order to determine the corresponding position of the sun (Gates 1980). Tests of stand density effects on leaf orientation were made with separate analyses of variance of the cosine of the angle of incidence (cos[i]) for each level in the canopy and part of the day.

Light measurements. Light interception was measured at 36 and 77 DAE. At 36 DAE, the canopy had just closed for the two lowest stand densities. Light measurements (quantum flux of photosynthetically active radiation, 400-700 nm) were made with a 80-cm Sunfleck Ceptometer (Decagon Devices Inc., Pullman, Washington) at solar noon (± 1 hour) under conditions in which direct solar radiation was not obscured by clouds. The sensors, spaced 1 cm apart, were oriented along a north to south line centered at the main stem of the individual plant being measured. At 36 DAE, before all the canopies closed, measurements

extended half the distance to the nearest neighbors to the north and the south, and were made at 10 cm increments from ground level to above the canopy. At 77 DAE, in the continuous closed canopies, all 80 sensors were used at each stand density, and measurements were made at 20 cm increments below the top of the canopy. Least squares estimates of the value K were based on separate analysis of variance models for LAI, NI, or depth-in-canopy as the independent variable and the logarithm of relative light level ($\ln I/I_0$) as the dependent variable. The test for interaction of the independent variable with stand density (heterogeneity of slopes) was the test of differential stand density effects on K.

RESULTS AND DISCUSSION

Leaf area. Both LAI and NI were significantly affected by stand density at 36 DAE, but were not different by 77 DAE (Table 4.1). The closed canopies were the result of the extensive branching at lower stand densities (Chapter 3). At 36 DAE, a greater proportion of the individual shoot's leaves (Figure 4.1) and leaf-bearing nodes (Figure 4.2) were located low on the shoot at lower stand densities. Differences among densities in shape of the distribution were the result of differences in the number of lateral branches formed along the lower main-stem nodes (Chapter 3). By 77 DAE, the additional vertical axes formed by the large lower branches produced distributions of leaf area and number of leaves that were shifted relatively upward on the shoot, as observed in sicklepod in monoculture or in competition with soybean (Sims and Oliver 1990). The profiles of LAI and NI at 77 DAE were similar in terms of distribution with height and total depth of canopy. Multiple regressions of leaf areas showed significant effects of stand density and depth in canopy at 36 and 77 DAE, but no difference between main-stem and branch leaf areas at 77 DAE. The additional leaves near the top of the 51 individual m^{-2} canopy at 77 DAE had only a small

Table 4.1. Leaf area index (LAI) and node index (NI) at 36 and 77 days after sicklepod emergence (DAE) for each sicklepod stand density[a].

Stand density	LAI 36 DAE	LAI 77 DAE	NI 36 DAE	NI 77 DAE
m^{-2}	$m^2\ m^{-2}$	$m^2\ m^{-2}$	nodes m^{-2}	nodes m^{-2}
51	3.8 (0.22)	7.4 (1.89)	1110 (84)	1340 (318)
18	2.8 (0.09)	7.1 (1.16)	933 (79)	1130 (164)
9	2.2 (0.09)	6.5 (0.78)	568 (36)	1010 (130)
5	1.2 (0.08)	8.7 (1.23)	340 (23)	1130 (140)

[a]Values are mean ($\pm$1 standard error). Stand density significantly affected LAI and NI at 36 DAE ($p < 0.001$ for each), but not at 77 DAE ($p = 0.664$ and 0.691, respectively)

Table 4.2. Area of individual leaves and length of petiole of main-stem leaves from nodes 6 through 9 at 36 days after emergence (DAE), and leaf area of randomly selected leaves at a canopy depth between 40 and 100 cm at 77 DAE[a].

Stand density	Leaf area 36 DAE	Petiole length 37 DAE	Leaf area 77 DAE
m^{-2}	cm^2	cm	cm^2
51	64.8 (2.42)	7.6 (0.12)	52.9 (6.32)
18	70.0 (1.48)	7.8 (0.22)	49.7 (3.13)
9	80.2 (2.81)	8.0 (0.18)	51.9 (2.29)
5	85.8 (1.73)	8.1 (0.26)	69.2 (2.49)

[a]Values are mean ($\pm$1 standard error). Stand density significantly affected leaf area at 36 and 77 DAE, and petiole length at 36 DAE ($p < 0.001$ for each).

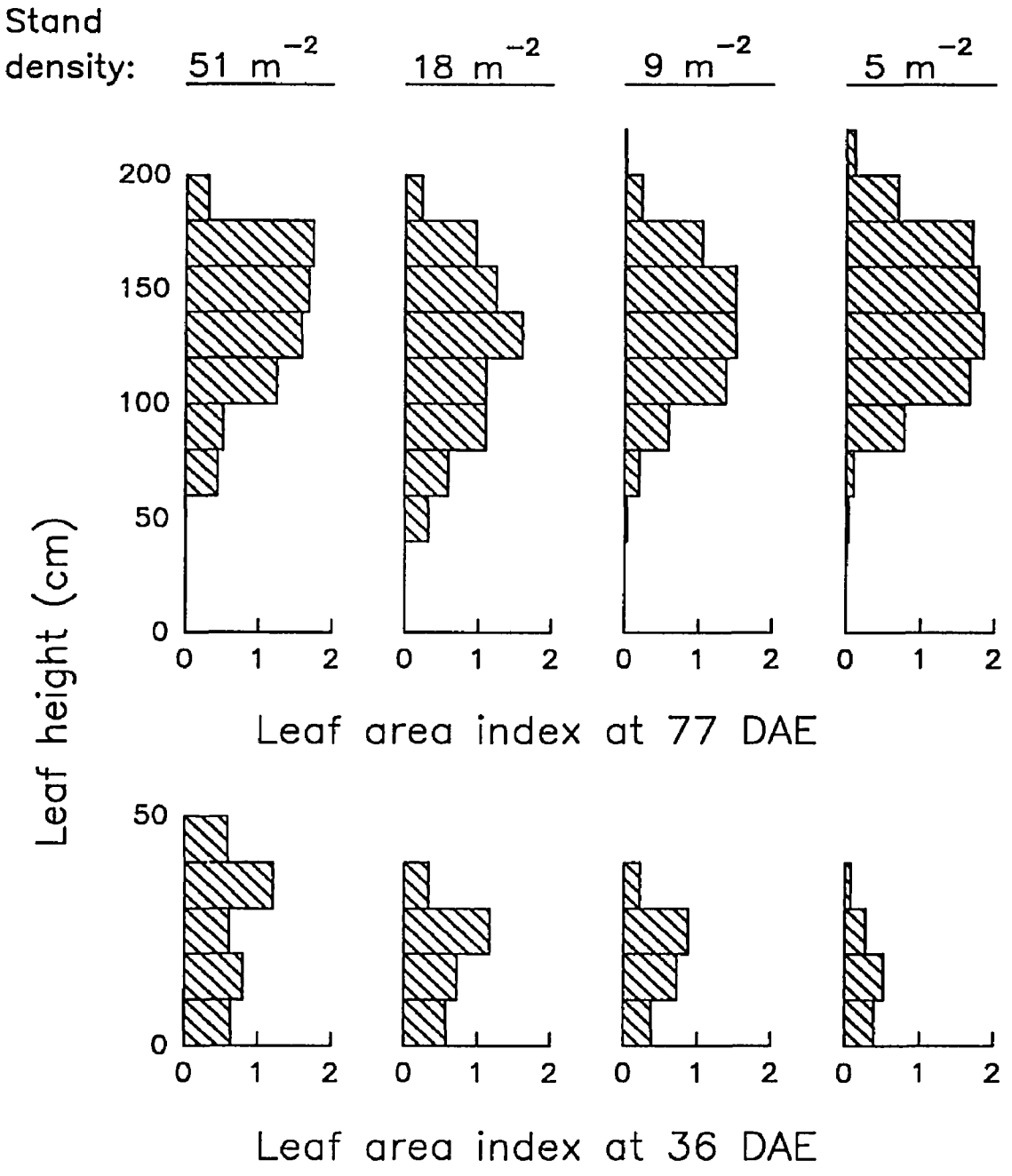

Figure 4.1. Stratified profiles of leaf area index (LAI) of sicklepod stands at 77 and 36 days after emergence (DAE; top and bottom row, respectively). Note: the vertical scales of the two rows are different.

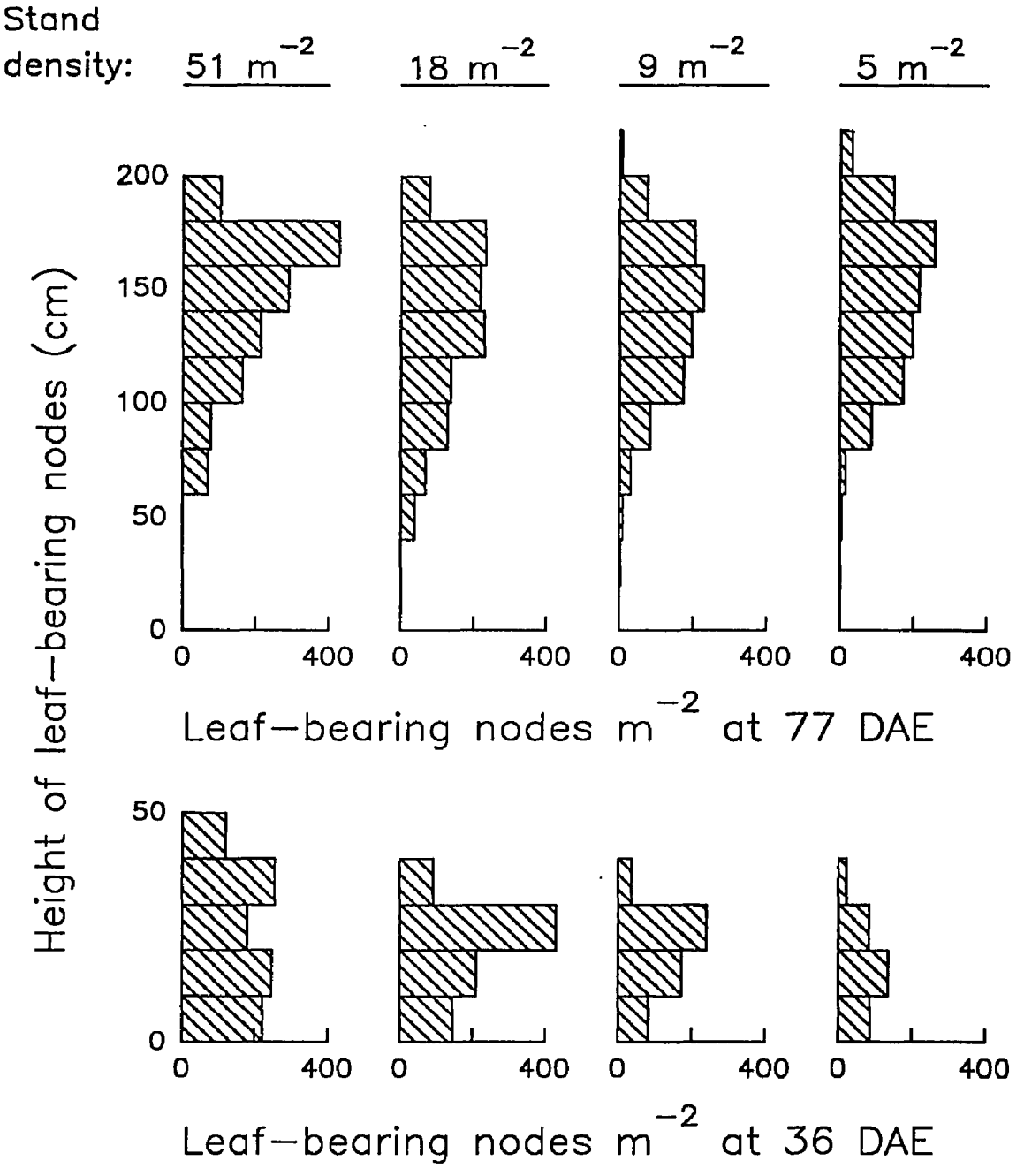

Figure 4.2. Stratified profiles of node index (NI; leaf-bearing nodes m^{-2}) of sicklepod stands at 77 and 36 days after emergence (DAE; top and bottom row, respectively). Note: the vertical scales of the two rows are different.

effect on total leaf area since leaves generally do not fully expand near the top of the canopy as upward growth ceases (Irwin and Barneby 1982, personal observation).

Area of individual leaves was affected by stand density, especially early in the season (Table 4.2). Leaf areas and petiole lengths on fully expanded leaves, near the top of the shoot at 36 DAE, were greater at lower stand densities; crowding within a stand can affect individual leaf area (Bunce 1990, Jurik 1991). Area of individual leaves sampled at 77 DAE were also significantly different, but this was not a progressive increase in area with decreased stand density as at 36 DAE.

Leaf orientation. Sicklepod leaves at the top of the canopy displayed diurnal leaf movement, while lower (30 cm below top) leaves showed very little movement (Figure 4.3). Stand density had no significant effect on cos[i] for leaves at the top of the canopy (Figure 4.3, A and B; $P > 0.05$). The only stand-density effect was between the lowest stand density and the others at mid-day, 30 cm below the top of the canopy (Figure 4.3D). The distribution of cos[i] for the lowest stand density relative to that of all stand densities is shown in Figure 4.3; since the distributions are so similar, the remainder of the discussion will consider the pooled data.

Leaf azimuth was randomly distributed (analyses not shown). While leaf movement maintained a distribution of leaf angles of incidence with a mean of approximately 60 degrees in upper leaves, the lack of detectable movement in lower leaves (leaves at 30 cm below top of canopy had leaf angles distributed around a mean zenith angle of approximately 40 degrees) resulted in constantly changing angles of incidence. The differential movement of leaves and sun resulted in mean cos[i] for leaves at the top of the canopy of 0.60 and 0.48 for morning and mid-day respectively (Figure 4.3, A and B); the mean cos[i] at 30 cm below the top of the canopy was 0.42 and 0.80 for morning and mid-day respectively (Figure 4.3,

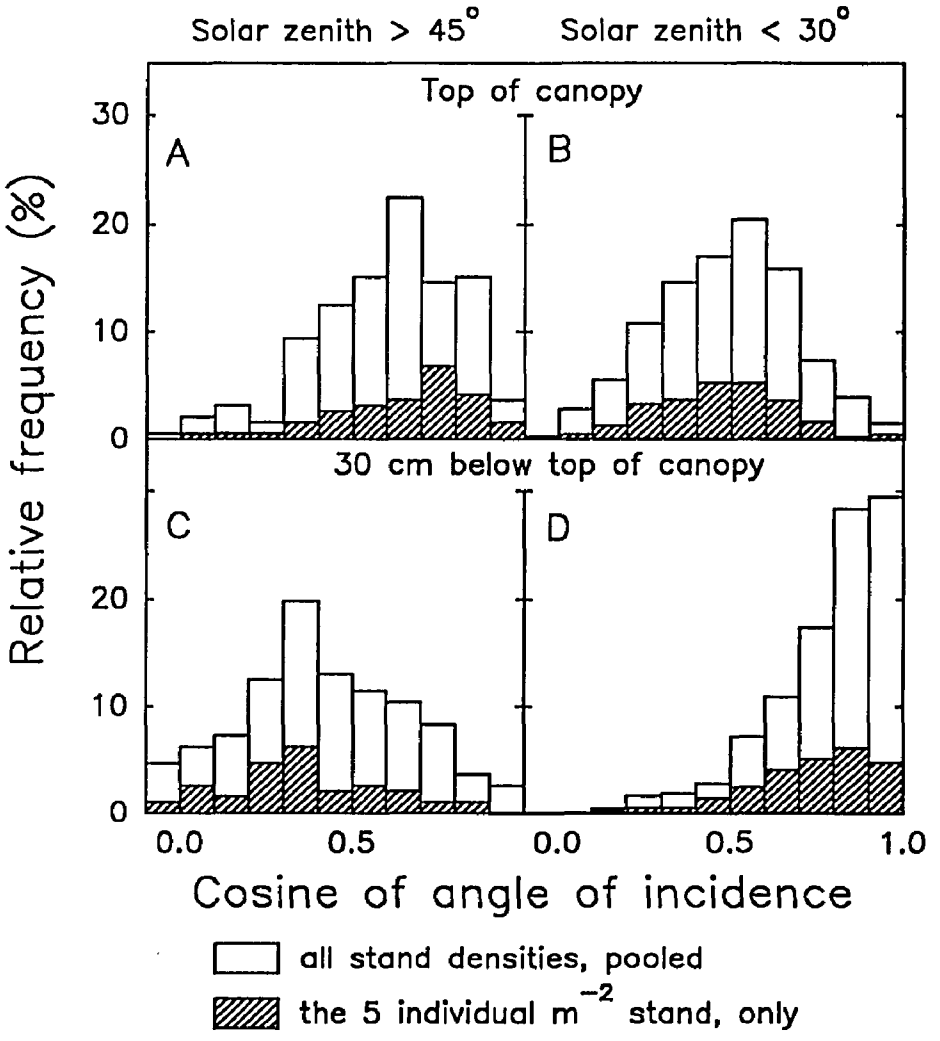

Figure 4.3. Frequency distributions of sicklepod leaf cosine of angle of incidence (for direct solar radiation; at 1.0 on abscissa the leaf directly faces the sun) at: (A and B) the top of the canopy, and (C and D) 30 cm below the top of the canopy at 36 days after emergence. Angles were measured in the morning (A and C, n=192 each; with solar zenith angle greater than 45°) and at mid-day (B and D, n=788 and 431 respectively; with solar zenith angle less than 30°).

C and D), reflecting the movement of the sun rather than any reorientation of leaves. The value of K for a population of leaves is equal to the linear average cos[i] when the model for canopy light interception uses Σ LAI to represent position in the canopy.

Through the middle of the day, the upper layer of leaves in the sicklepod canopy would intercept about the same proportion of light as would a canopy with randomly oriented leaves (K=0.50; Monteith and Unsworth 1990). The lack of movement in the more horizontally distributed lower leaves, resulting in a greater mid-day cos[i], resulted in these leaves intercepting 60% more light than would random oriented leaves. Diurnal, light driven, leaf movements often produce altered distributions of light and photosynthetic rates within the canopy (Koller 1990, Fu and Ehleringer 1991). Sicklepod shows an apparently similar response to light level during the period through the middle of the day when light levels are greatest. The transition in cos[i], with depth in the canopy, results in an arrangement of canopy leaves that approaches an ideal configuration as suggested by Myneni et al. (1986); the canopy has mostly vertically oriented leaves in the upper canopy and progressively increases cos[i] (leaves more horizontal) toward the bottom of the canopy, thus light would be uniformly intercepted over the whole canopy.

In addition to the potential advantage in light distribution through the leaf mass conferred by the arrangement of leaf angles with depth, the leaf angles at a particular level determine the distribution of light levels across photosynthetic leaf surfaces. A comparison of the top of the sicklepod canopy, mid-day distribution, with that from a randomly distributed leaf mass will be used to illustrate the point. Leaves in a randomly distributed canopy would have a uniform distribution over all values of cos[i] between zero and one, with mean cos[i]=0.50 (Monteith and Unsworth 1990); this is compared to the relatively narrower distribution (Figure 4.3B) around a mean cos[i]=0.48 in sicklepod. Relative

photosynthesis, at the two leaf angle distributions, were calculated by summing estimated photosynthetic rates over these frequency distributions. Estimates of typical photosynthetic response to light, by a C_3 plant, were based on the soybean model of Harley et al. (1985; from equation by Smith 1937) with maximal gross uptake and respiration of CO_2 set at 20 and 3 μmol m^{-2} s^{-1}, respectively. Despite essentially the same amount of light intercepted per unit leaf surface, sicklepod had an 8% greater photosynthetic rate due to the different distribution of light levels over the leaf surfaces. The basis for the different photosynthesis with similar light interception was due to the narrower distribution of cos[i]. Relatively fewer leaves intercepted light at very low cos[i] (low photosynthetic rates) and few intercepted light at high cos[i] (above light saturated photosynthetic rates).

Light interception. Light measurements were made at various strata in the 36 and 77 DAE canopies and used to estimate a coefficient of light interception (K). Three values of K were estimated: K_{LAI}, based on cumulative LAI; K_{NI}, based on cumulative NI, and K_D, based on depth in the canopy (Table 4.3). This produced the three models of I/I_o: $\exp(-K_{LAI} \cdot \Sigma \text{ LAI})$, $\exp(-K_{NI} \cdot \Sigma \text{ NI})$, and $\exp(-K_D \cdot \text{depth})$. Stand density did not have a significant effect on K_{LAI}, K_{NI}, or K_D at 36 or 77 DAE ($P > 0.05$ for each), although there appeared to be considerably more variability at 36 DAE than at 77 DAE.

The residuals from the least square regressions of $\ln(I/I_o)$ as a function of LAI and NI were very evenly and narrowly distributed (regression mean square errors of 0.0251 and 0.0258, respectively), indicating a nearly linear relationship used for the estimate of K; but this was not the case for the relationship of $\ln(I/I_o)$ with depth in the canopy (regression mean square error was over tenfold greater (0.2846). Therefore, the use of a single K_{LAI} or K_{NI} as an estimate of light interception within the sicklepod canopy appears to be appropriate despite the differences between top-of-canopy and 30-cm-depth leaf angle distributions at 36 DAE.

Table 4.3. Coefficients of light interception for each of the sicklepod stand densities at 36 and 77 days after emergence; the coefficients: K_{LAI}, K_{NI}, and K_D are based on position in canopy expressed as leaf area index, node index, and depth, respectively. Mean values of K and their associated 95% confidence limits are given for 77-DAE canopies.

Stand	K_{LAI}	K_{NI}	K_D
m^{-2}	$m^2\ m^{-2}$	$m^2\ node^{-1}$	cm^{-1}
36 days after emergence			
51	0.441	0.00149	0.0399
18	0.833	0.00256	0.0635
9	0.448	0.00167	0.0328
5	0.566	0.00217	0.0306
77 days after emergence			
51	0.420	0.00300	0.0119
18	0.465	0.00335	0.0146
9	0.468	0.00330	0.0148
5	0.383	0.00332	0.0155
Mean K at 77 days after emergence			
Upper 95% limit	0.478	0.00355	0.0163
Mean K	0.443	0.00325	0.0142
Lower 95% limit	0.408	0.00295	0.0121

The values of K_{NI} were applied to estimates of light extinction in the sicklepod stands (26 m^{-2}) added to soybean in Chapter 2. At 84 days after sicklepod emergence, modeled light levels at the top of the soybean canopy were 10 to 14% of ambient, if the sicklepod emerged with the soybean; and 19 to 24% of ambient if the sicklepod emerged seven days after the sicklepod. Since large lateral branches, originating low along the main-stem, contributed substantially to the number of leaves in the sicklepod canopy above the soybean, competition from soybean that reduces these branches should increase light to the soybean canopy (Chapter 2). If narrow row-spacing of soybean reduced branching of all sicklepod to a level similar to those located 13 cm from the soybean row, K_{NI}-based estimates of light level show 23 and 62% increases in light at the top of the soybean canopy for sicklepod emerging with and seven days after soybean, respectively.

The larger leaves at lower stand densities may have provided individual shoots greater light interception before the canopy closed. Leaf angles at the top of the shoot provided a relatively high transmission of light at mid-day; thus, the more horizontal lower leaves were exposed to higher light levels. The use of a calibrated K_{NI} to estimate light interception within a sicklepod canopy appeared to be an accurate alternative to K_{LAI}.

Chapter 5. Conclusions

Sicklepod leaf area, internode elongation, node production, and, in particular, early branching were affected by the level of competition (distance to neighbors) with either soybean or other sicklepod. While lower, early-formed, branches produced more leaves and extended out a greater distance from the main-stem with greater distance to neighbors, most of these branches also extended to the top of the canopy on all sicklepod. Upper main-stem branches were not affected by distance to neighbor. An increase in crowding in the stand, associated with decreased distance to neighbors, tended to decrease the number of large vertical axes added by the lower branches, and thus limited lateral expansion of individual shoots. Large lower branches contributed a substantial portion of leaves in the sicklepod canopy formed over the soybean. Hence, the number of leaves placed in the canopy above soybean by an individual sicklepod was very dependent on the effects of early competition on branch formation. Sicklepod emerging on a soybean row produced fewer branches, and, as a consequence, exerted almost no area-of-influence on the soybean row, despite being taller than the soybean. The relationship between early competitive effects on branching and later canopy formation suggests an advantage of planting narrow soybean rows so that lower branches of sicklepod are reduced.

Branch formation at lower main-stem nodes was the first response to distance to neighbors apparent in sicklepod seedlings. Branching was initiated early, at nodes just below the shoot apex, and branching frequency was inversely proportional to the relative level of competition at the time branches were produced. Differences in rate of branching and outward direction of branch growth were measurable even before the effects of crowding altered shoot height or number of leaves. However, outward growth appeared to be the first

priority after sicklepod emergence. Removal of neighboring plants, or planting adjacent to soybean rows, did not lead to directional shoot growth, so that sicklepod growth and shoot structure appeared to respond to overall space available, but not to directional asymmetry of the space.

Sicklepod monocultures eventually formed relatively uniform, closed, canopies, with similar light interception characteristics. Monoculture stands were basically similar, in growth and shoot structure, to sicklepod in stands added to soybean; this suggested that light interception characteristics would also be similar. The distributions of leaf area and leaf orientation within an individual sicklepod shoot produced relatively constant rates of light interception over leaf area through the canopy. Light interception, commonly modeled using leaf area index, was successfully modeled on the basis of the simpler index, number of leaves per unit area. When used in conjunction with experimental data for sicklepod interference, this simpler model of light availability to the crop may be a more practical means of predicting yield losses due to shading.

Literature Cited

Acock, B., and M. C. Acock. 1987. Periodic shading and the location and timing of branches in soybean. Agronomy Journal 79:949-952.

Akey, W. C., T. W. Jurik, and J. Dekker. 1990. Competition for light between velvetleaf (Abutilon theophrasti) and soybean (Glycine max). Weed Research 30:403-411.

Baldocchi, D. D., S. B. Verma, N. J. Rosenberg, B. L. Bland, and J. E. Specht. 1985. Microclimate-plant architectural interactions: influence of leaf width on the mass and energy exchange of a soybean canopy. Agricultural and Forest Meteorology 35:1-20.

Ballaré, C. L., R. A. Sánchez, A. L. Scopel, J. J. Casal, and C. M. Ghersa. 1987. Early detection of neighbour plants by phytochrome perception of spectral changes in reflected sunlight. Plant, Cell and Environment 10:551-557.

Ballaré, C. L., A. L. Scopel, and R. A. Sánchez. 1989. Photomodulation of axis extension in sparse canopies. Plant Physiology 89:1324-1330.

Ballaré, C. L., A. L. Scopel, and R. A. Sánchez. 1990. Far-red radiation from adjacent leaves: an early signal of competition in plant canopies. Science 247:329-332.

Ballaré, C. L., A. L. Scopel, and R. A. Sánchez. 1991. Photocontrol of stem elongation in plant neighbourhoods: effects of photon fluence rate under natural conditions of radiation. Plant, Cell and Environment 14:57-65.

Banks, P. A., T. N. Tripp, J. W. Wells, J. E. Hammel. 1985. Effects of tillage on sicklepod (Cassia obtusifolia) interference with soybeans (Glycine max) and soil water use. Weed Science 34:143-149.

Barnes, P. W., W. Beyschlag, R. Ryel, S. D. Flint, and M. M. Caldwell. 1990. Plant competition for light analyzed with a multispecies canopy model. III. Influence of canopy structure in mixtures and monocultures of wheat and wild oat. Oecologia 82:560-566.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, London, England.

Bazzaz, F. A., and J. L. Harper. 1977. Demographic analysis of the growth of Linum usitatissimum. New Phytologist 78:193-208.

Bozsa, R. C., L. R. Oliver, and T. L. Driver. 1989. Intraspecific and interspecific sicklepod (Cassia obtusifolia) interference. Weed Science 37:670-673.

Bridges, D. C., and R. H. Walker. 1985. Influence of weed management and cropping systems on sicklepod (Cassia obtusifolia) seed in the soil. Weed Science 33:800-804.

Buchanan, G. A., and E. R. Burns. 1971. Weed competition in cotton I. Sicklepod and tall morninglory. Weed Science 19:576-579.

Bunce, J. A. 1990. The effect of leaf size on mutual shading and cultivar differences in soybean leaf photosynthetic capacity. Photosynthesis Research 23:67-72.

Byrd, J. D., and H. D. Coble. 1991. Interference of selected weeds in cotton (Gossypium hirsutum). Weed Technology 5:263-269.

Casal, J. J., R. A. Sánchez, and V. A. Deregibus. 1986. The effect of plant density on tillering: the involvement of R/FR ratio and the proportion of radiation intercepted per plant. Environmental and Experimental Botany 26:365-371.

Elmore, C. D. 1986. Weed survey - southern states. Southern Weed Science Society Research Report 39:136.

Firbank, L. G., and A. R. Watkinson. 1987. On the analysis of competition at the level of the individual plant. Oecologia 71:308-317.

Fisher, J. B. 1986. Branching patterns and angles in trees. Pages 493-523. in T. J. Givnish, editor. On the economy of plant form and function. Cambridge University Press, Cambridge, England.

Franco, M. 1986. The influence of neighbours on the growth of modular organisms with an example from trees. Philosophical Transactions of the Royal Society London B 313:200-225.

Fu, Q. A., and J. R. Ehleringer. 1991. Modification of paraheliotropic leaf movements in Phaseolus vulgaris by photon flux density. Plant, Cell and Environment 14:339-343.

Gates, D. M. 1980. Biophysical Ecology. Springer-Verlag, New York, USA.

Geber, M. A. 1989. Interplay of morphology and development on size inequality: a Polygonum greenhouse study. Ecological Monographs 59:267-288.

Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. Ecology 68:1211-1223.

Gurevitch, J., P. Wilson, J. L. Stone, P. Teese, and R. J. Stoutenburgh. 1990. Competition among old-field perennials at different levels of soil fertility and available space. Journal of Ecology 78:727-744.

Harley, P. C., J. A. Weber, and D. M. Gates. 1985. Interactive effects of light, leaf temperature, CO_2 and O_2 on photosynthesis in soybean. Planta 165:249-263.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, England.

Irwin, H. S., and R. C. Barneby. 1982. The american cassiinae. A synoptical revision of leguminosae tribe cassieae subtribe cassiinae in the new world. Memoirs of the New York Botanical Garden 35(1):252-255.

James, K. L., P. A. Banks, and K. J. Karnok. 1988. Interference of soybean, Glycine max, cultivars with sicklepod, Cassia obtusifolia. Weed Technology 2:404-409.

Jones, M. 1985. Modular demography and form in silver birch. Pages 223-237 in J. White, editor. Studies on plant demography. A festschrift for John L. Harper. Academic Press, London, England.

Jones, M., and J. L. Harper. 1987a. The influence of neighbours on the growth of trees. I. The demography of buds in Betula pendula. Proceedings of the Royal Society London B 232:1-18.

Jones, M., and J. L. Harper. 1987b. The influence of neighbours on the growth of trees. II. The fate of buds on long and short shoots in Betula pendula. Proceedings of the Royal Society London B 232:19-33.

Jurik, T. W. 1991. Population distributions of plant size and light environment of giant ragweed (Ambrosia trifida L.) at three densities. Oecologia 87:539-550.

Kasperbauer, M. J. 1987. Far-red light reflection from green leaves and effects on phytochrome-mediated assimilate partitioning under field conditions. Plant Physiology 85:350-354.

Kaul, K., and M. J. Kasperbauer. 1988. Row orientation effects on FR/R light ratio, growth and development of field-grown bush bean. Physiologia Plantarum 74:415-417.

Koller, D. 1990. Light-driven leaf movements. Plant, Cell and Environment 13:615-632.

Legere, A. and M. M. Schreiber. 1989. Competition and canopy architecture as affected by soybean (Glycine max) row width and density of redroot pigweed (Amaranthus retroflexus). Weed Science 37:84-92.

Lemeur, R., and B. L. Blad. 1974. A critical review of light models for estimating the shortwave radiation regime of plant canopies. Agricultural Meteorology 14:255-286.

Lovell, P. H., and P. J. Lovell. 1985. The importance of plant form as a determining factor in competition and habitat exploration. Pages 209-221. in J. White, editor. Studies on plant demography. A festschrift for John L. Harper. Academic Press, London, England.

Maillette, L. 1982. Structural dynamics of silver birch. I. The fate of buds. Journal of Applied Ecology 19:203-218.

Maillette, L. 1985. Modular demography and growth patterns of two annual weeds (Chenopodium album L. and Spergula arvensis L.) in relation to flowering. Pages 239-255 in J. White, editor. Studies on plant demography. A festschrift for John L. Harper. Academic Press, London, England.

Maillette, L. 1986. Canopy development, leaf demography and growth dynamics of wheat and three weed species growing in pure and mixed stands. Journal of Applied Ecology 23:929-944.

Matlack, G. R., and J. L. Harper. 1986. Spatial distribution and the performance of individual plants in a natural population of Silene dioica. Oecologia 70:121-127.

McWhorter, C. G., and G. L. Sciumbato. 1988. Effects of row spacing, benomyl, and duration of sicklepod (Cassia obtusifolia) interference on soybean (Glycine max) yields. Weed Science 36:254-259.

Miller, T. E., and J. Weiner. 1989. Local density variation may mimic effects of asymmetric competition on plant size variability. Ecology 70:1188-1191.

Mithen, R., J. L. Harper, and J. Weiner. 1984. Growth and mortality of individual plants as a function of "available area." Oecologia 62:57-60.

Monks, D. W., and L. R. Oliver. 1988. Interactions between soybean (Glycine max) cultivars and selected weeds. Weed Science 36:770-774.

Monteith, J. L., and M. H. Unsworth. 1990. Principles of environmental physics. Second edition. Edward Arnold, London, England.

Myneni, R. B., G. Asrar, G. W. Wall, E. T. Kanemasu, and I. Impens. 1986. Canopy architecture, irradiance distribution on leaf surfaces and consequent photosynthetic efficiencies in heterogeneous plant canopies. Part II. Results and Discussion. Agricultural and Forest Meteorology 37:205-218.

Myneni, R. B., J. Ross, and G. Asrar. 1989. A review on the theory of photon transport in leaf canopies. Agricultural and Forest Meteorology 45:1-153.

Novoplansky, A., D. Cohen, and T. Sachs. 1989. Ecological implications of correlative inhibition between plant shoots. Physiologia Plantarum 77:136-140.

Novoplansky, A., D. Cohen, and T. Sachs. 1990. How portulaca seedlings avoid their neighbors. Oecologia 82:490-493.

Pike, D. R., E. W. Stoller, and L. M. Wax. 1990. Modeling soybean growth and canopy apportionment in weed-soybean (Glycine max) competition. Weed Science 38:522-527.

Radosevich, S. R., and J. S. Holt. 1984. Weed ecology, implications for vegetation management. John Wiley and Sons, New York, USA.

Regnier, E. E., and E. W. Stoller. 1989. The effects of soybean (Glycine max) interference on the canopy architecture of common cocklebur (Xanthium strumarium), jimsonweed (Datura stramonium), and velvetleaf (Abutilon theophrasti). Weed Science 37:187-195.

Retzinger, J. E. 1984. Growth and development of sicklepod (Cassia obtusifolia) selections. Weed Science 32:608-611.

Rice, S. A., and F. A. Bazzaz. 1989. Quantification of plasticity of plant traits in response to light intensity: comparing phenotypes at a common weight. Oecologia 78:502-507.

Ross, J. 1981. The radiation regime and architecture of plant stands. W. Junk, The Hague, The Netherlands.

Ross, M. A., and J. L. Harper. 1972. Occupation of biological space during seedling establishment. Journal of Ecology 60:77-88.

Roush, M. L. and S. R. Radosevich. 1985. Relationships between growth and competitiveness of four annual weeds. Journal of Applied Ecology 22:895-905.

Shaw, D. R., S. A. Bruff, and C. A. Smith. 1991. Effect of soybean (Glycine max) row spacing on chemical control of sicklepod (Cassia obtusifolia). Weed Technology 5:286-290.

Silander, J. A., and S. W. Pacala. 1985. Neighborhood predictors of plant performance. Oecologia 66:256-263.

Sims, B. D., and L. R. Oliver. 1990. Mutual influences of seedling johnsongrass (Sorghum halepense), sicklepod (Cassia obtusifolia), and soybean (Glycine max). Weed Science 38:139-147.

Smith, E. 1937. The influence of light and carbon dioxide on photosynthesis. General Physiology 20:807-830.

Smith, B. H. 1984. The optimal design of a herbaceous body. The American Naturalist 123:197-211.

Smith, H. 1982. Light quality, photoreception, and plant strategy. Annual Review of Plant Physiology 33:481-518.

Smith, H., J. J. Casal, and G. M. Jackson. 1990. Reflection signals and the perception by phytochrome of the proximity of neighbouring vegetation. Plant, Cell and Environment 13:73-78.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, the principles and practice of statistics in biological research. Second edition. W. H. Freeman, New York, New York, USA.

Somda, Z. C., and S. J. Kays. 1990. Sweet potato canopy architecture: branching pattern. Journal of the American Society of Horticulture Science 115:33-38.

Sprugel, D. G., T. M. Hinckley, and W. Schaap. 1991. The theory and practice of branch autonomy. Annual Review of Ecology and Systematics 22:309-334.

Stoller, E. W., and J. T. Woolley. 1985. Competition for light by broadleaf weeds in soybeans (Glycine max). Weed Science 33:199-202.

Stützel, H., and W. Aufhammer. 1991. Canopy development of a determinate and an indeterminate cultivar of Vicia faba L. under contrasting plant distributions and densities. Annals of Applied Biology 118:185-199.

Teem, D. H., C. S. Hoveland, and G. A. Buchanan. 1980. Sicklepod (Cassia obtusifolia) and coffee senna (Cassia occidentalis) geographic distribution, germination, and emergence. Weed Science 28:68-70.

Thurlow, D. T., and G. A. Buchanan. 1972. Competition of sicklepod with soybeans. Weed Science 20:379-384.

Tomlinson, P. B. 1982. Chance and design in the construction of plants. Pages 162-186 in R. Sattler, editor. Axioms and principles of plant construction. W. Junk, The Hague, The Netherlands.

Walker, R. H., M. G. Patterson, E. Hauser, D. J. Isenhour, J. W. Todd, and G. A. Buchanan. 1984. Effects of insecticide, weed-free period, and row spacing on soybean (Glycine max) and sicklepod (Cassia obtusifolia) growth. Weed Science 32:702-706.

Waller, D. M. 1986. The dynamics of growth and form. Pages 291-320 in M. J. Crawley, editor. Plant ecology. Blackwell Scientific Publications, Oxford, England.

Waller, D. M., and D. A. Steingraeber. 1985. Branching and modular growth: Theoretical models and empirical patterns. Pages 225-257 in J.B.C. Jackson, L.W. Buss, and R.E. Cook, editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.

Weiner, J. 1982. A neighborhood model of annual-plant interference. Ecology 63:1237-1241.

Weiner, J. and S. C. Thomas. 1986. Size variability and competition in plant monocultures. Oikos 47:211-222.

Weiner, J., G. M. Berntson, and S. C. Thomas. 1990. Competition and growth form in a woodland annual. Journal of Ecology 78:459-469.

White, J. 1979. The plant as a metapopulation. Annual Review of Ecology and Systematics 10:109-145.

Zaffaroni, E., and A. A. Schneiter. 1989. Water-use efficiency and light interception of semidwarf and standard-height sunflower hybrids grown in different row arrangements. Agronomy Journal 81:831-836.

Appendix. Additional Tables and Figures

Table A.1. Number of leaves, dry weight of leaves and rate of survival (in stands only) of sicklepod shoots at day 84 (after sicklepod emergence) for sicklepod in stands and day 92 for widely spaced sicklepod[a].

Treatment		Number of leaves[b]	Dry weight of leaves	Percent of plants surviving
			g	
1988 and 1990 sicklepod in stands with soybean				
0 DAS	13 CFS	25 (3.4)	4.9 (0.48)	87
	38 CFS	32 (6.0)	6.1 (0.58)	82
7 DAS	13 CFS	15 (3.3)	2.4 (0.37)	75
	38 CFS	34 (6.7)	6.2 (0.96)	80
1988 sicklepod in stands without soybean				
			7.6 (0.45)	81
1990 widely spaced sicklepod				
0 CFS		117 (28.9)	18.0 (4.57)	
5 CFS		118 (42.0)	19.4 (8.31)	
25 CFS		180 (21.9)	27.2 (2.24)	

[a]Notation for treatments: CFS, cm from soybean row; DAS, days after soybean emergence. Values are means (±1 standard error).

[b]Determined in 1990 only.

Table A.2. Dry weights of soybean at 128 days after emergence for 20 cm sections of row centered at 0, 20, 40, 60, and 80 cm along row from the individual sicklepod shoot[a].

Distance from row	Position of 20 cm segment of row				
	0	20	40	60	80
	g	g	g	g	g
Total dry weight					
0	242 (46.0)	210 (27.1)	235 (13.1)	201 (25.7)	236 (28.3)
5	193 (38.1)	247 (21.8)	228 (29.8)	208 (19.5)	236 (30.5)
25	203 (42.6)	212 (25.6)	244 (48.8)	199 (37.5)	212 (33.1)
No sicklepod	251 (51.3)	248 (15.8)	232 (24.5)	218 (47.6)	251 (26.8)
Dry weight of pods only					
0	72 (13.8)	66 (7.6)	69 (4.6)	60 (7.1)	71 (8.5)
5	56 (11.5)	71 (7.0)	70 (9.3)	72 (10.9)	72 (8.9)
25	56 (11.3)	61 (8.9)	81 (12.3)	68 (12.6)	67 (9.1)
No sicklepod	73 (14.7)	76 (5.5)	75 (9.8)	65 (14.1)	76 (8.0)

[a]Values are means (±1 standard error).

Table A.3. Coefficients for correlation between shoot dry weight at 76 days after emergence (DAE) and components of sicklepod shoot structure at 36 and 20 DAE for sicklepod grown in monocultures at 51, 18, 9, and 5 individuals m^{-2}[a].

Stand density	Shoot height	Number of main-stem nodes	Number of primary branches	Number of leaves
m^{-2}	cm			
Shoots at 36 DAE				
51	0.25	0.72*	-0.02	-0.12
18	0.51	0.72*	0.75*	0.82**
9	0.72**	0.51	-0.11	0.46
5	0.13	0.10	0.09	-0.48
Shoots at 20 DAE				
51	0.39	0.41	-0.65*	0.07
18	0.74**	0.72*	0.60*	0.38
9	0.75**	0.69**	0.45	0.82**
5	-0.28	0.06	-0.56	-0.15

[a]Levels of significance: * $P<0.05$, ** $P<0.01$.

Table A.4. Shoot dry weight and height of six nearest neighbors of focus individuals (used for description of shoot structure) of sicklepod in monoculture stands at 51, 18, 9, and 5 individuals m^{-2}. Weight was measured at 76 days after emergence (DAE), and height was measured at 20, 36, and 76 DAE in both 1989 and 1990[a].

Stand density	Shoot dry weight	Height		
		20 DAE	36 DAE	76 DAE
m^{-2}	g	cm	cm	cm
51	16 (1.1)	9 (0.5)	45 (1.9)	136 (6.0)
18	40 (3.4)	8 (0.4)	38 (2.8)	148 (4.9)
9	77 (3.2)	9 (0.3)	36 (1.1)	144 (5.3)
5	149 (13.2)	8 (0.3)	34 (1.4)	144 (8.9)

[a]Values are means (± mean standard error per year).

Table A.5. Number of branches and individual branch dry weight of individual, widely-spaced, sicklepod added to soybean stand. Measurements were made at 92 days after soybean emergence; branches were classified as growing either toward or away from soybean row[a].

Distance from soybean row	Number of branches		Branch dry weight	
	toward soybean	away from soybean	toward soybean	away from soybean
m^{-2}			g	g
5	8.1 (1.85)	10.8 (0.96)	5.7 (2.06)	6.0 (2.01)
25	9.7 (0.78)	9.4 (1.46)	6.2 (1.23)	5.2 (0.94)

[a]Values are means (± 1 standard error).

Table A.6. Characteristics of branches growing toward and away from gap in the 9 individual m^{-2} sicklepod stand at 25, 29, and 33 days after emergence[a].

Position relative to opening	Length of branch	Number of nodes	Radial distance to branch apex	Height of branch apex	Angle of node 1 with main-stem	Angle of apex with main-stem
	cm		cm	cm	deg.	deg.
33 days after emergence						
away from	12 (0.7)	3.8 (0.16)	10 (0.6)	15 (1.0)	57 (2.1)	55 (2.2)
toward	12 (0.8)	3.7 (0.18)	10 (0.7)	13 (0.7)	62 (1.1)	59 (1.1)
29 days after emergence						
away from	6 (0.7)	2.8 (0.22)	5 (0.6)	9 (0.5)	55 (2.1)	54 (1.9)
toward	6 (0.6)	2.6 (0.15)	5 (0.5)	8 (0.5)	53 (2.4)	51 (1.9)
25 days after emergence						
away from	4 (0.0)	2.0 (0.0)	3 (0.2)	5 (0.6)	53 (3.8)	53 (3.8)
toward	3 (0.3)	2.0 (0.0)	3 (0.2)	4 (0.4)	56 (5.2)	56 (5.2)

[a]Values are means (± 1 standard error).

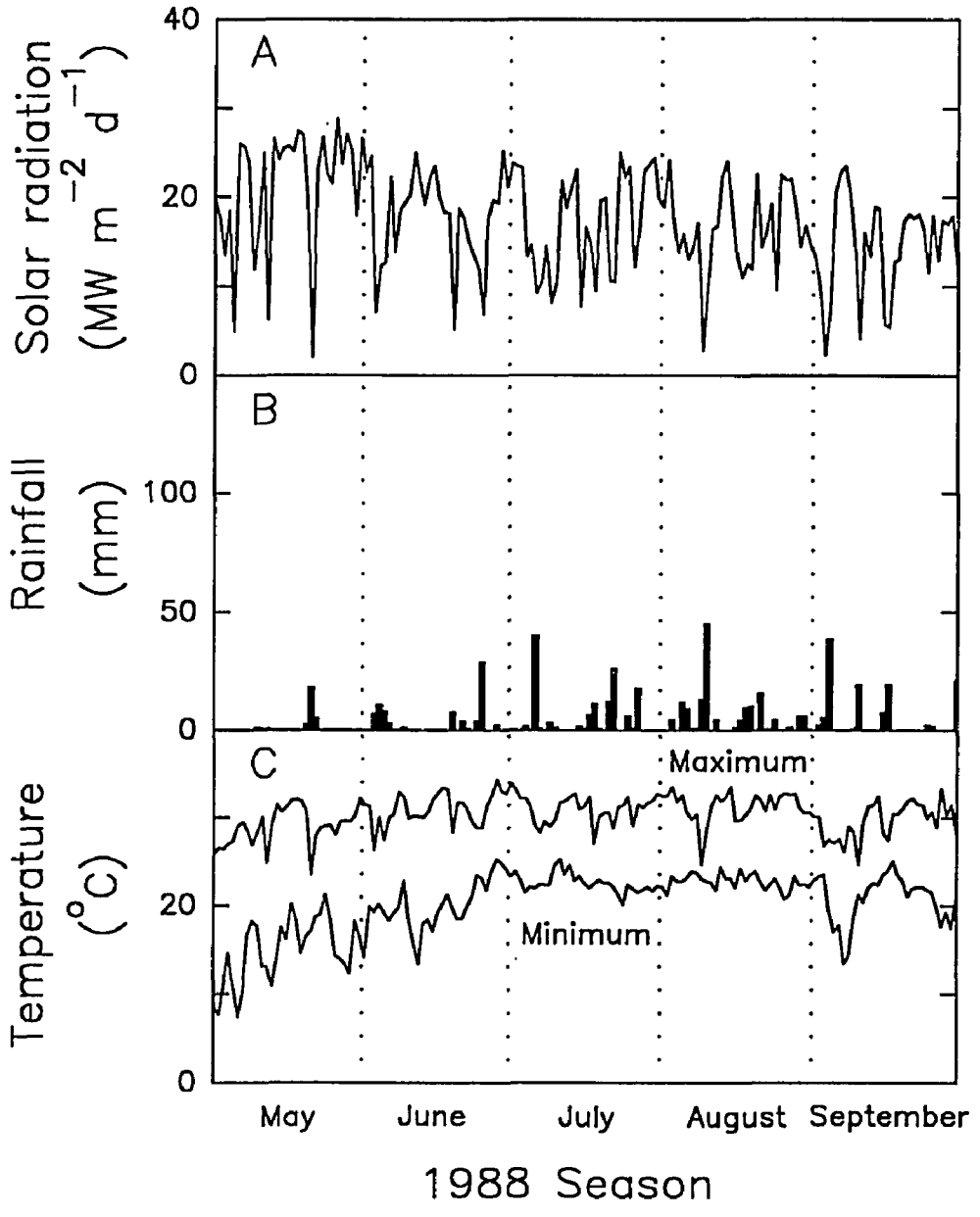

Figure A.1. Daily weather summaries of (A) solar radiation, (B) rainfall, and (C) maximum and minimum temperature at the Plant Science Farm, Central Station, Baton Rouge, Louisiana, for the 1988 season.

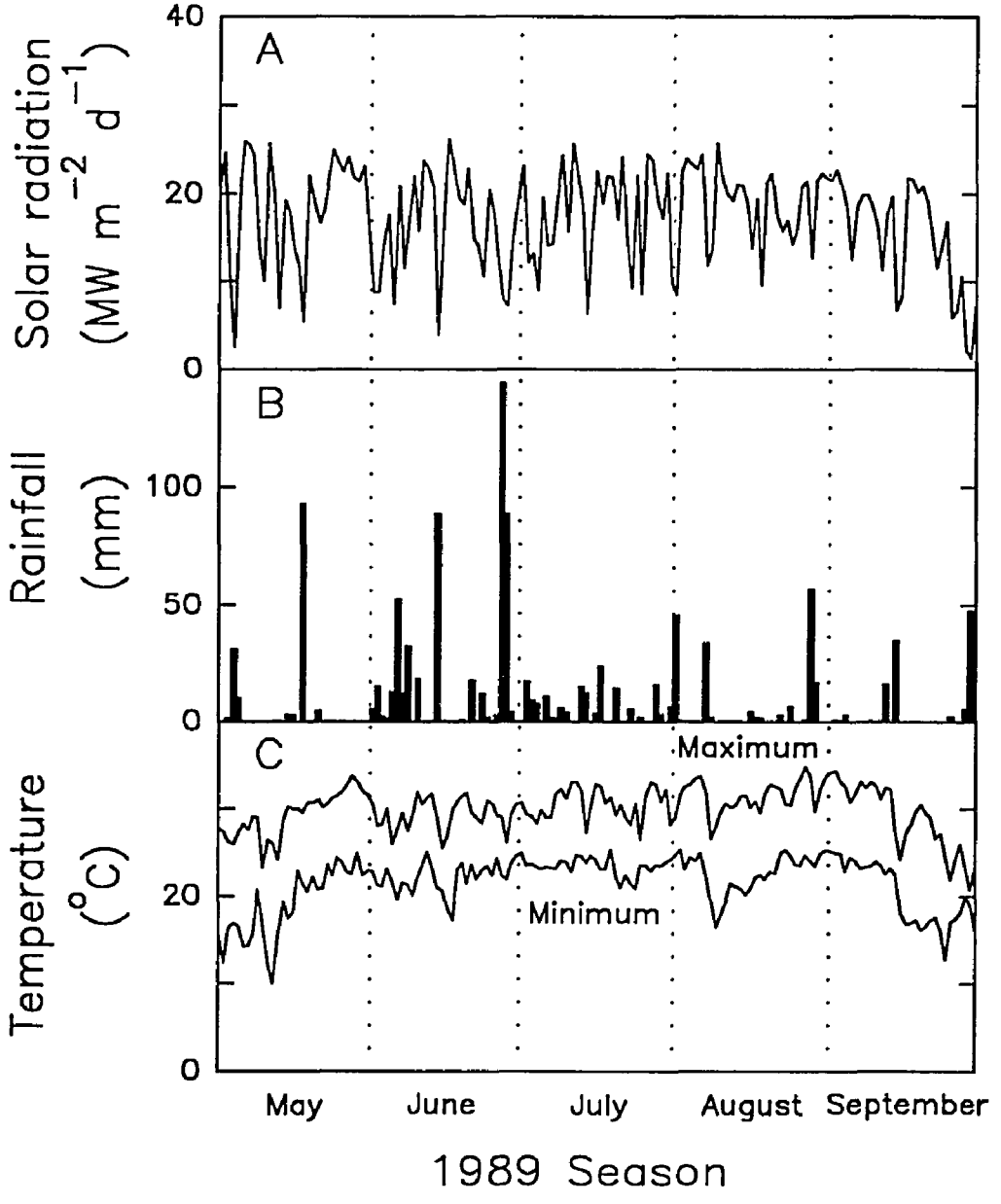

Figure A.2. Daily weather summaries of (A) solar radiation, (B) rainfall, and (C) maximum and minimum temperature at the Plant Science Farm, Central Station, Baton Rouge, Louisiana, for the 1989 season.

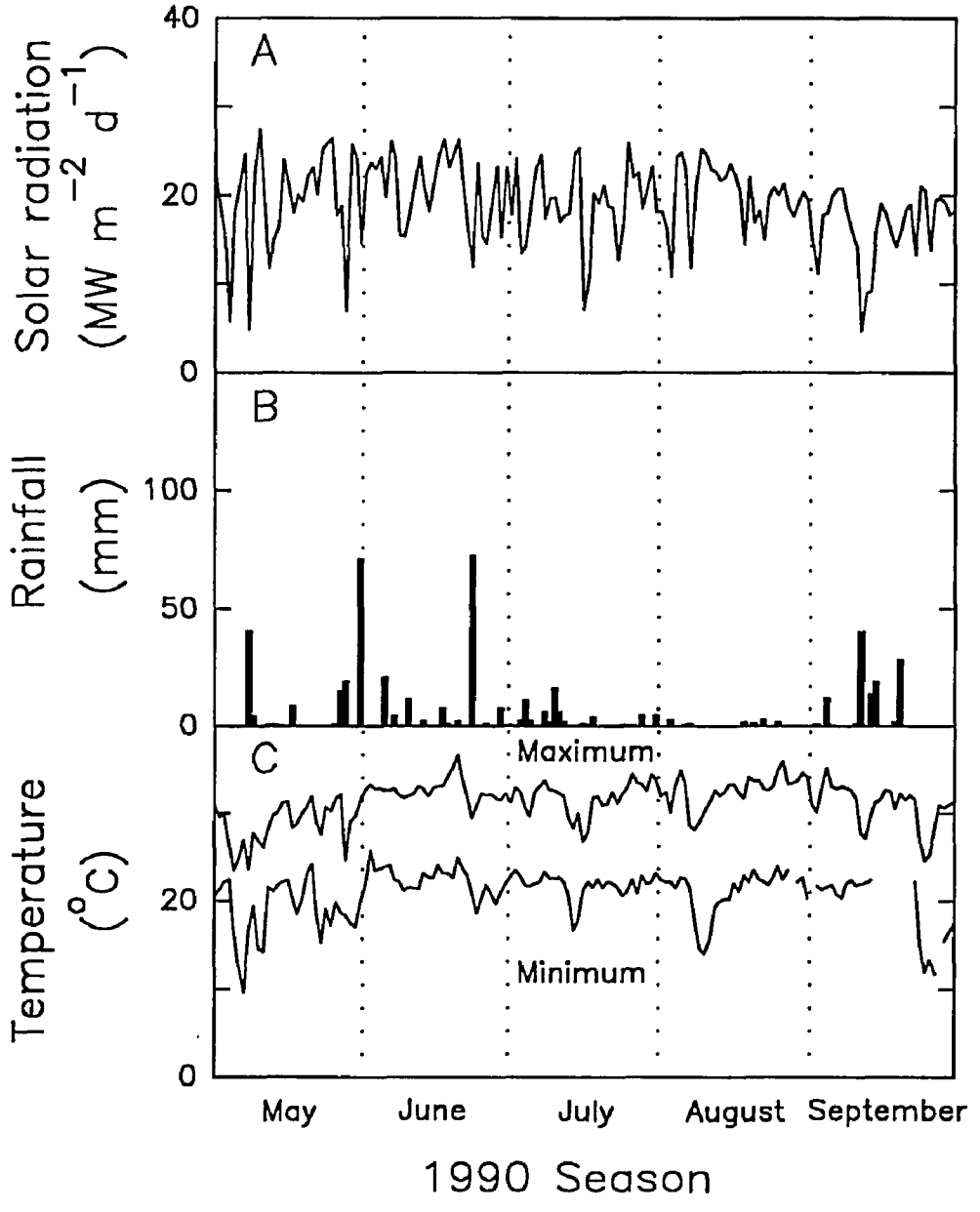

Figure A.3. Daily weather summaries of (A) solar radiation, (B) rainfall, and (C) maximum and minimum temperature at the Plant Science Farm, Central Station, Baton Rouge, Louisiana, for the 1990 season.

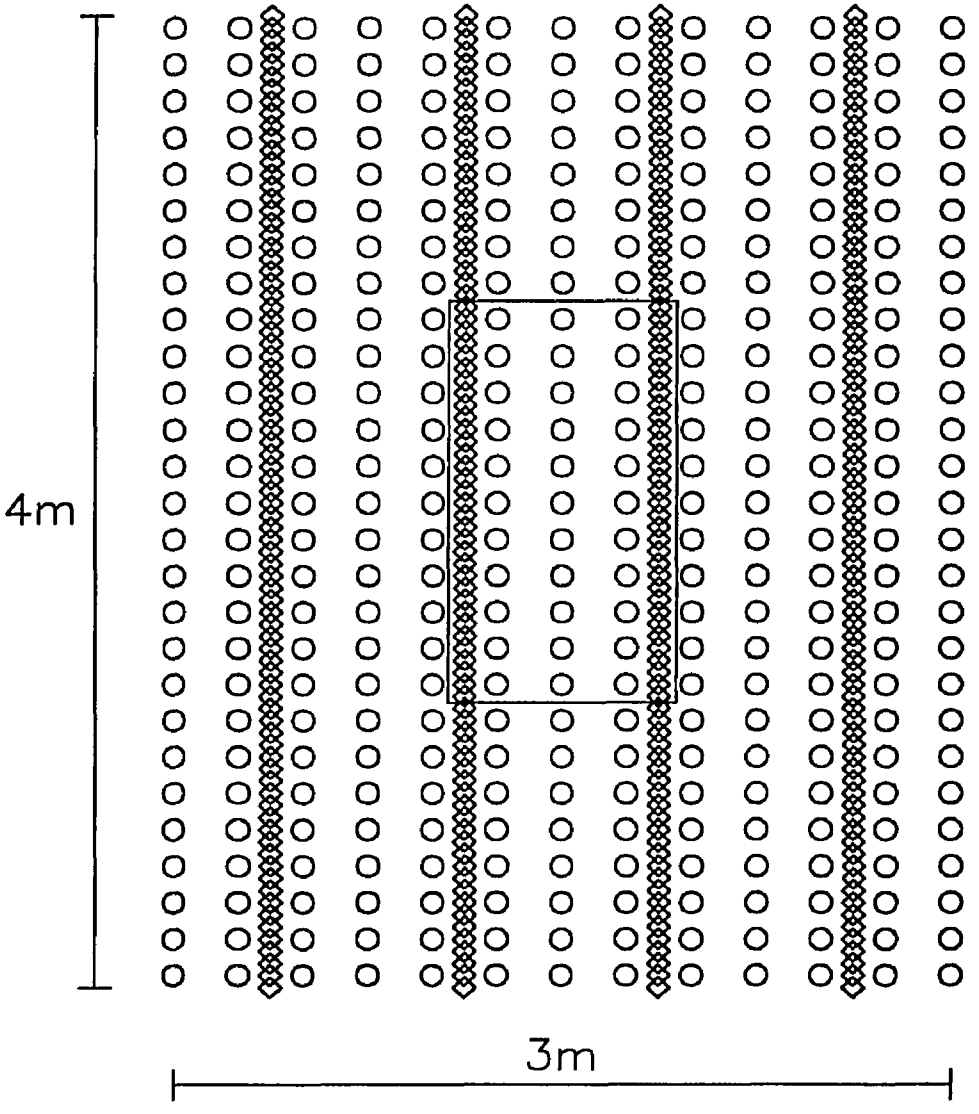

Figure A.4. Diagram of typical plot arrangement for sicklepod stands added to soybean. Rows of diamonds signify soybean rows and circles represent position of individual sicklepod. The framed area in the center of the plot represents the sampling area.

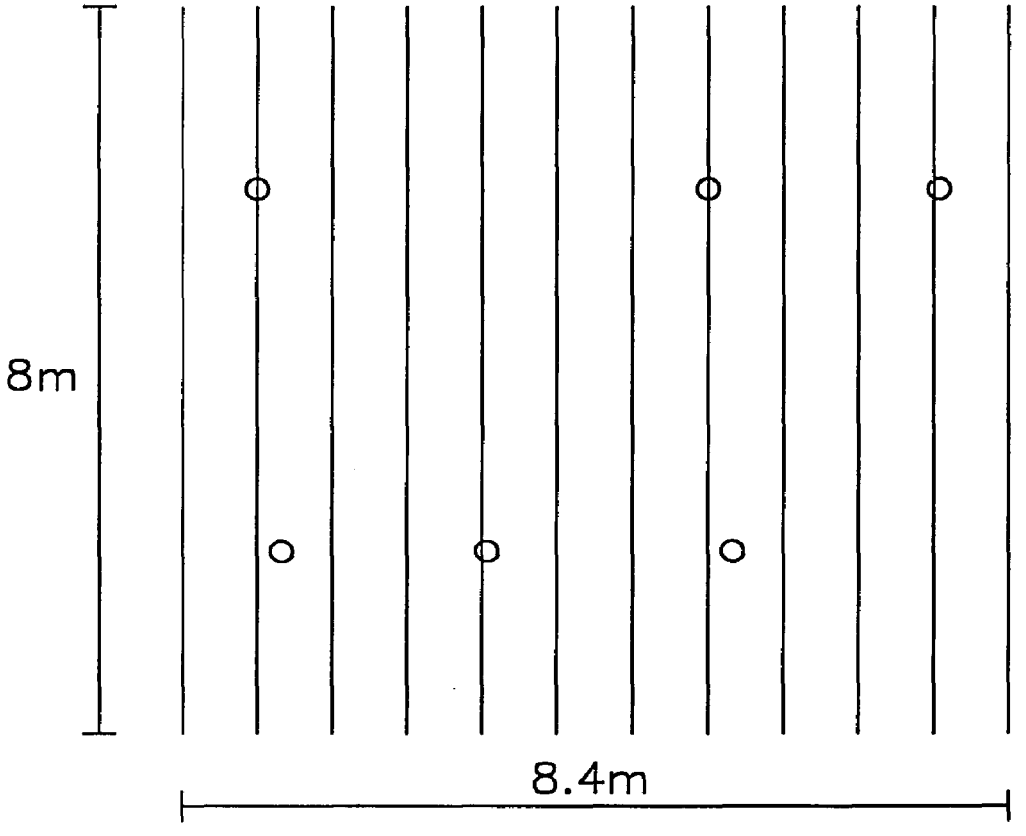

Figure A.5. Diagram of typical arrangement of individual widely spaced sicklepod added to soybean. Lines signify soybean rows and circles represent position of individual sicklepod located on, or at 5 or 25 cm from, the soybean row.

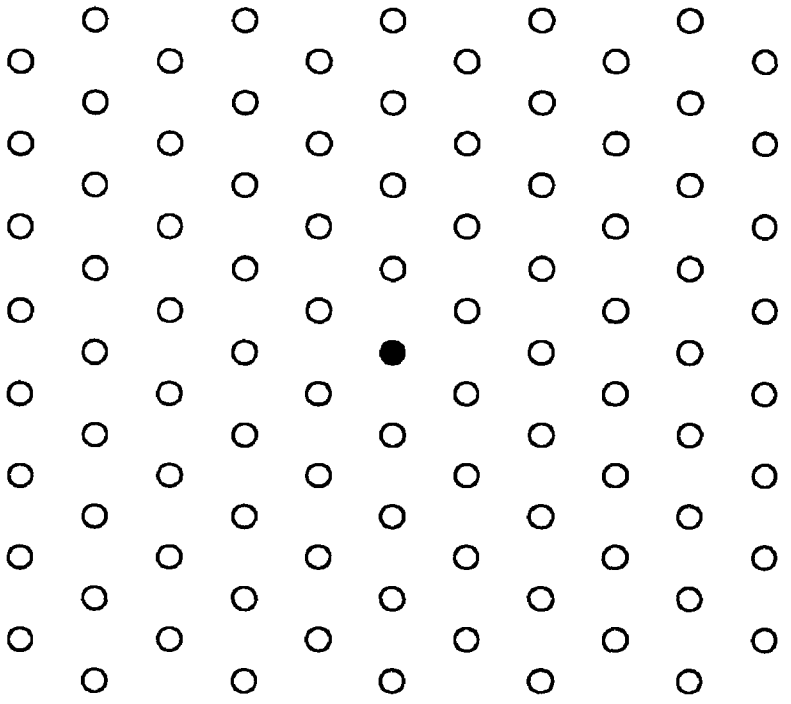

Figure A.6. Diagram of typical plot arrangement of sicklepod monocultures. Circles represent positions of individual sicklepod located 15, 25, 35, or 50 cm apart.

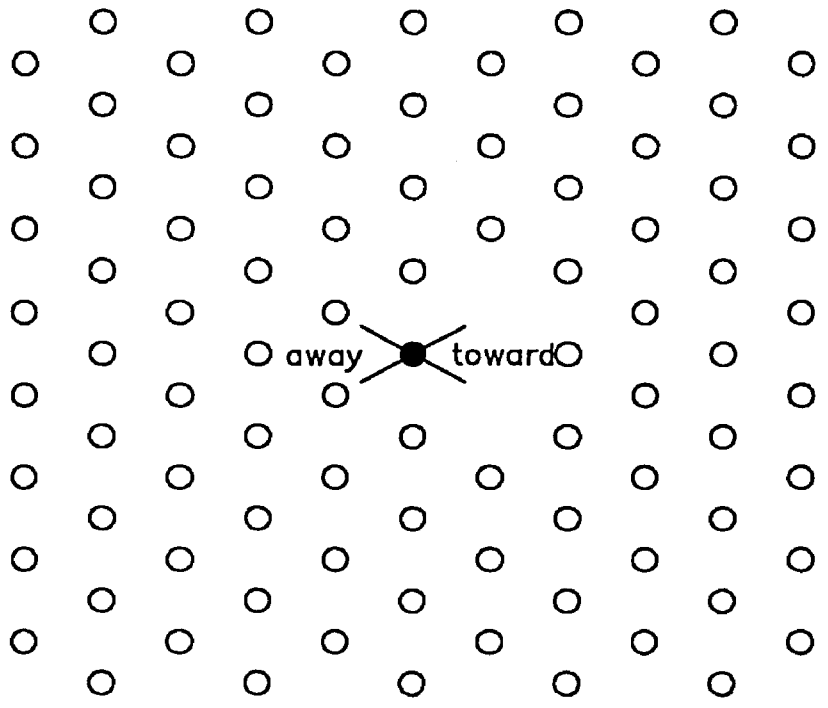

Figure A.7. Diagram of typical plot arrangement of sicklepod in monoculture located adjacent to a gap in the stand. Circles represent positions of individual sicklepod located 35 cm apart. Sampling of branches concentrated on those located within the 60° arcs oriented either directly toward or away from the gap.

Stand densities:

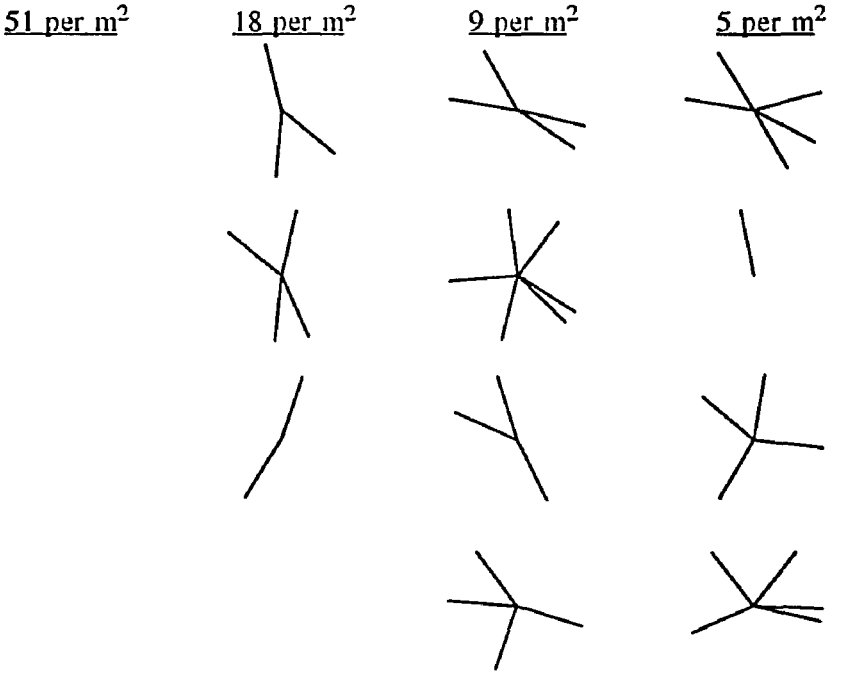

Figure A.8. Diagrams indicating azimuths of primary branches on sicklepod shoots at 36 days after emergence in the sicklepod monocultures in 1989. Figures are positioned so that north is toward the top of the page.

Stand densities:

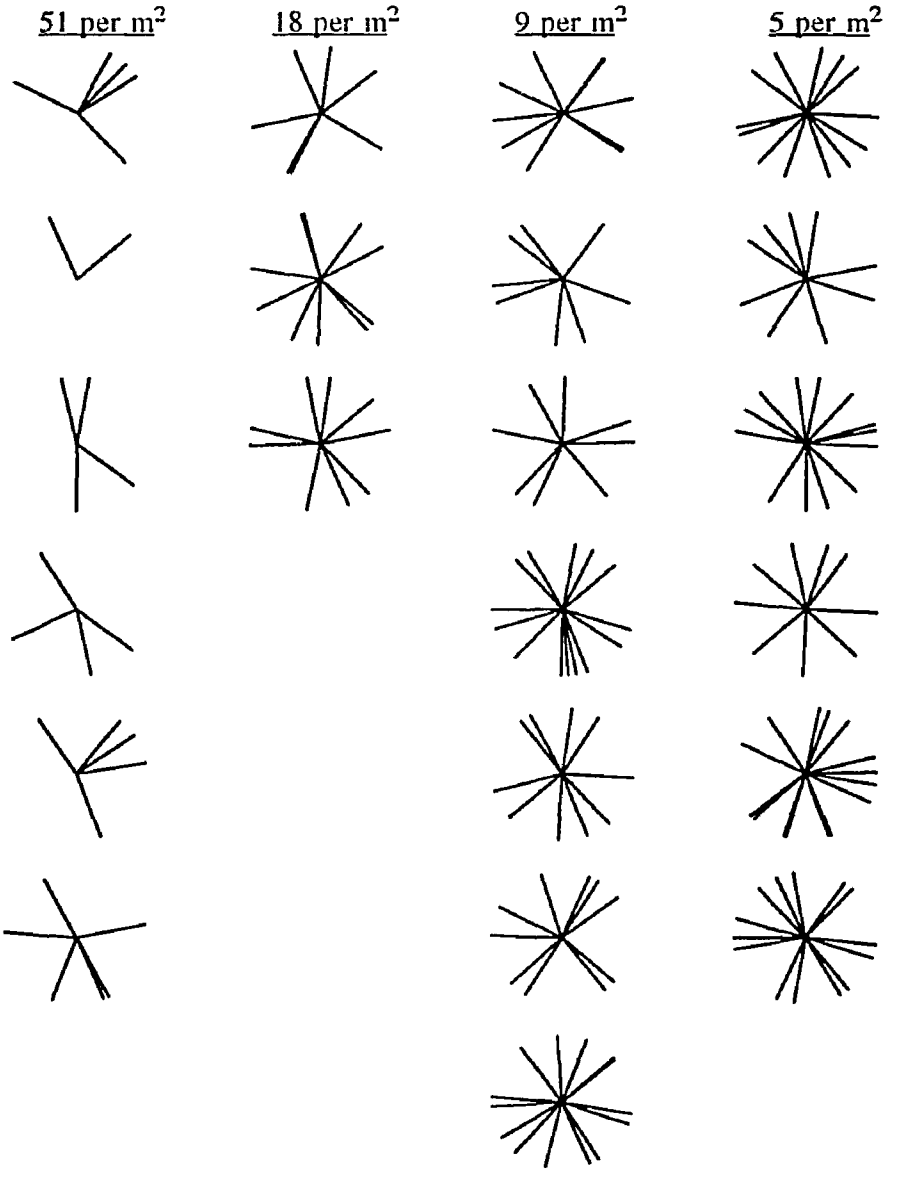

Figure A.9. Diagrams indicating azimuths of primary branches on sicklepod shoots at 36 days after emergence in the sicklepod monocultures in 1990. Figures are positioned so that north is toward the top of the page.

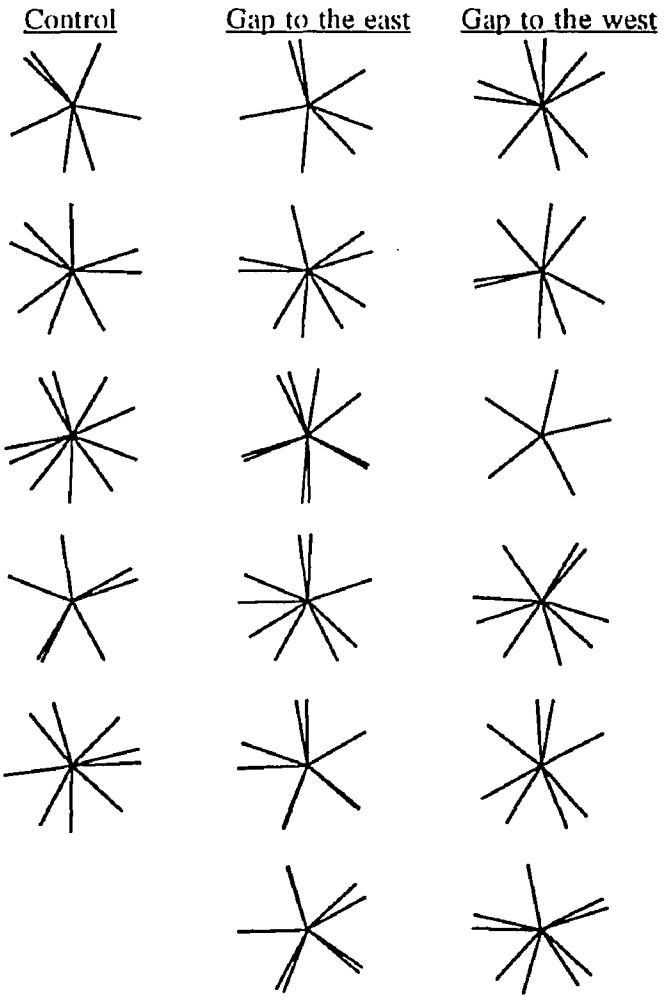

Figure A.10. Diagrams indicating azimuths of primary branches on sicklepod shoots at 33 days after emergence in the sicklepod located adjacent to a gap in the stand. Figures are positioned so that north is toward the top of the page.

Vita

James E. Smith was born in Grand Rapids, Michigan on September 20, 1956. He received his primary and secondary education in Dallas, Texas. Undergraduate education, at Rice University in Houston, Texas, concluded with a Bachelor of Arts degree in 1982, with a major in biology. Graduate work was at Louisiana State University in Baton Rouge, Louisiana. In 1985, he received a Master of Science degree in botany. He is currently a candidate for a doctorate degree with a major in plant health and a minor in botany.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: James E. Smith

Major Field: Plant Health

Title of Dissertation: Shoot Growth and Form of Senna obtusifolia in Response to Soybean and Intraspecific Competition

Approved:

Peter W. Jordan
Major Professor and Chairman

Daniel Fogel
Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

April 1, 1992